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Editor of *Northwest Science*

David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, AR-10
Seattle, Washington 98195
Telephone: 206-543-1587
Fax: 206-685-0790
Internet: wild@u.washington.edu

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Announcements

Editor's Note

You will notice a few changes in this issue of *Northwest Science*. First of all, we have a new cover design that will bring a little more life to the exterior of the journal. There is also a change on the inside pages of *Northwest Science*: a new section called "Northwest Science Forum." This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged in order to foster an ongoing discussion. Readers are encouraged to be creative, articulate, and passionate in this section. The Forum will not be peer-reviewed in order to expedite publication. I hope that you will find this new section of the journal to be enjoyable and stimulating. Most importantly, I encourage you to participate and add your ideas to the discussion.

Arthur R. Tiedemann, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, Oregon 97850 and

James O. Klemmedson, School of Renewable Natural Resources, 325 Biological Sciences, East Building, University of Arizona, Tucson, Arizona 85721

The Influence of Western Juniper Development on Soil Nutrient Availability

Abstract

The objective of the research reported here was to assess the effect of western juniper (*Juniperus occidentalis* Hook.) invasion and tree aging on soil nutrient availability in sagebrush/grass ecosystems of central Oregon. Barley was used as a bioassay test plant to determine availabilities of N, P, K, and S. The surface 15 cm of soil from beneath juniper canopies (canopy soil) and intercanopy areas (intercanopy soil) was collected for five age classes of trees ranging from 36 to 160 y. Nutrient availability determined by bioassay in these soils was compared to an area where juniper had not invaded. Phosphorus availability of intercanopy soils was significantly reduced for the two oldest tree classes. This result suggested an alteration of P availability by the lateral root system of western juniper in the intercanopy areas that is linked to juniper maturity. In canopy soils, juniper did not influence N availability. Advancing juniper maturity was associated with increasing then decreasing P availability with the oldest tree class. The most striking effect of juniper was increased S availability in canopy soils with advancing juniper maturity. Differential responses of N and S availability in canopy soils may reflect the fact that N mineralization is chiefly a biological process whereas S mineralization is both biological and biochemical. Low inherent availabilities of N and S suggest that productivity enhancement measures should include fertilization with these elements.

Introduction

The western juniper (*Juniperus occidentalis* Hook.) vegetation type occupies about 1.2 million ha in central and south-central Oregon (Dealy *et al.* 1978). Over much of its range, western juniper is expanding into the big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) vegetation type (Caraher 1978, Eddleman 1987). This invasion may be accompanied by redistribution of nutrients among biotic and abiotic compartments of these systems (Tiedemann 1987). Shallow lateral roots of juniper that extend well beyond the canopy edge (Young *et al.* 1984, Everett *et al.* 1986) may enable juniper to exploit moisture and nutrients from a much greater area than that within the canopy projection area.

Concern for western juniper invasion and the impact on forage production has resulted in management aimed at reducing the influence of western juniper. Juniper removal is accomplished by burning (Martin 1978), chaining and dozing (Winegar and Elmore 1978), fuelwood harvest (personal observations of the authors), and recently, whole tree harvesting for fuel for electric power generation (personal communication, Dr. Lee Eddleman, Professor, Oregon State University). Chaining, dozing, and fuelwood harvest often

are followed by burning of residues. Understanding nutrient accumulation and cycling patterns is an essential step in assessing the consequences of various management strategies on sustainable productivity of semiarid woodlands such as western juniper. If a large proportion of the nutrients on a site are incorporated into aboveground biomass compartments, whole-tree removal or burning of residues could result in large losses of nutrients and may impair future productivity (Tiedemann 1987).

Results reported here are part of a larger study to determine the influence of western juniper invasion and development on nutrient accumulation patterns in sagebrush/grass ecosystems (Cooperative State Research Service grant No. 87-CRSR-2-3116, Influence of Western Juniper Invasion on Nutrient Accumulation in Sagebrush/grass Ecosystems, A. R. Tiedemann and J. O. Klemmedson, Principal Investigators). Hypotheses relevant to the present study are that: 1) the lateral root system of western juniper exploits available nutrients in the intercanopy spaces, and the degree of change is related to the elapsed time of juniper development; and 2) nutrient accumulation by litterfall and a microenvironment more favorable for accumulation and maintenance of organic matter and nutrients (Jenny 1930, Tiedemann and Klemmedson 1986) in the area

beneath juniper canopies results in changes in availability of nutrients in that location (Tiedemann and Klemmedson 1973, Barth 1980, Everett *et al.* 1986, Klopatek 1987).

Our objective was to determine changes in availability of N, P, K, and S associated with invasion and development of western juniper over time by using bioassay of soil beneath juniper canopies and in intercanopy areas.

The Study Area

We conducted this study in central Oregon because it has the greatest concentration of western juniper (Driscoll 1964). The study area is at the Three Springs Ranch about 14 km south of Prineville, Oregon, in sections 11, 14, 23, and 27 T16S, R15E.

Climate is continental with maritime influence from storms originating off the Pacific coast (Driscoll 1964). The semiarid climate is characterized by dry, hot summers and cold winters with most of the precipitation as snow during the winter months and rain during spring and fall. Mean annual temperature at the airport approximately 7 km SW of Prineville is 9.5°C; mean January and July temperatures are 0°C and 19.5°C, respectively (United States Department of Commerce, National Oceanic and Atmospheric Administration 1973). Mean annual precipitation is 25.3 cm.

Soils are derived from Mount Mazama ash and are relatively young. Mount Mazama erupted about 6600 y b.p. (Baldwin 1964) depositing ash over basalt of local origin (United States Department of Agriculture, Soil Conservation Service 1986). Soils are Xerollic Camborthids of the Deschutes Series. Texture is uniformly sandy loam; depth ranges from 30 to 50 cm. The massive nature of the Mazama ash fall has resulted in uniform soil over large areas (United States Department of Agriculture, Soil Conservation Service 1986). No apparent buried soil exists over the basalt bedrock. Outcrops of basalt rock (blisters) are scattered throughout the area suggesting that the terrain was gently undulating prior to the Mazama ash fall.

Vegetation of the understory is dominated by big sagebrush, rabbitbrush (*Chrysothamnus spp.*), bluebunch wheatgrass, and Idaho fescue (*Festuca idahoensis* Elmer). Cover of understory vegetation is highly variable, but averages about 25%.

Procedures

Conceptual Approach

Following the state factor approach of Jenny (1961) and Major (1951), the conceptual model for this study,

$$N_{av}, P_{av}, K_{av}, S_{av} = f(o_j, t)_{cl, o, r, p}$$

states that availability of N, P, K, and S are a function of juniper invasion (o_j) and time (t) of juniper occupancy of a site, while state factors of climate (cl), biotic factor other than juniper (o), topography (r), and parent material (p) are held constant, or nearly so. Using this model, we carried out field sampling with rigid control of cl , o , r , and p such that their effect would be small relative to the effect of o_j and t .

For the small study area, climate, topography (<5% uniform eastward slope) and parent material were very uniform. Understory vegetation of shrubs and herbs was variable, and the impact of the biotic factor other than juniper (i.e., herbivores, humans, fire) appeared to be slight; in neither case did the distribution of the biotic subfactors appear to be related to juniper presence or size. Although shrubs and herbs may influence distribution of soil and litter nutrients (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Klemmedson 1983), the scale of distribution is small relative to that of western juniper and was controlled by sample location.

The study area showed no evidence of recent domestic grazing or disturbance to the area beneath trees. Evidence of firewood removal was sparse.

We selected five separate replicate sites for sampling, all within a distance of 8 km. At each replicate site, we selected three trees in each of five size (age) classes and randomly selected one tree in each size (age) class for sampling. This resulted in a total of 25 sample trees—five replications of five size (age) class western juniper. These are referred to as tree class 1 through 5.

At each of the five sites, we selected a 5 to 10 ha open area with no juniper invasion that we refer to as "No Juniper." Within each open area, three plots were established by random distance and direction from a central starting point. One plot was randomly selected from these for sampling.

Tree ages were determined from sections taken from the butt section of trees cut as part of the larger study. Samples were aged by Franco Biondi,

Laboratory of Tree Ring Research, University of Arizona. Average tree age ranged from 36 y for tree class 1 to 160 y for tree class 5 (Table 1). Average height ranged from 3.3 to 9.9 m.

A sample of soil about 30 by 30 cm to 15-cm depth was collected from each of the following locations at each site: a distance of 0.5 canopy radius due north from the base of each western juniper; 4.0 canopy radii due north from the base of each tree (intercanopy); and at the selected sample plot in the open site ("No Juniper").

TABLE 1. Average age and height of 5 classes of western juniper sample trees.

Tree class	Age	— yr	Height	— m
	Average	Range	Average	Range
1	36	21-58	3.3	2.9-3.8
2	52	36-68	4.8	4.1-6.0
3	62	41-85	7.0	5.7-8.2
4	81	44-135	9.5	8.5-11.7
5	160	108-231	9.9	9.2-10.4

Bioassay Trial

A bioassay trial (Jenny *et al.* 1950) was used to determine availabilities of individual nutrients N, P, K, and S. Soils were air-dried, mixed thoroughly, and sieved to remove particles larger than 4 mm. The five field sites served as replications for the greenhouse bioassay trial. Soil (400 g) was weighed into plastic pots to which the following nutrient treatments were applied:

TREATMENT	NUTRIENTS ADDED
Control	No added nutrients
No nitrogen (N ₀)	P, K, S
No phosphorus (P ₀)	N, K, S
No potassium (K ₀)	N, P, S
No sulfur (S ₀)	N, P, K,
Full nutrient treatment	N, P, K, S

Nitrogen was added at a rate of 134 mg.kg⁻¹ as ammonium nitrate; phosphorus at 89 mg.kg⁻¹ as calcium dihydrogen phosphate; potassium at 45 mg.kg⁻¹ as potassium chloride; and sulfur at 45 mg.kg⁻¹ as magnesium sulfate. These sources of P and S offer little risk of confounding with Ca and Mg, which are rarely deficient in western soils, with some exceptions such as serpentine soils and highly leached, acid soils (Bohn *et al.*, 1979).

Barley seeds were sown into the pots, thinned to three plants per pot, and grown in a controlled environment chamber with 12-hour photoperiod with full spectrum, high output fluorescent lamps at 24°C daytime and 19°C nighttime temperatures. Relative humidity was maintained at about 70% during the growth period. After 8 weeks, plants were harvested, oven-dried at 70°C and weighed.

Study design was a split-split plot with trees (tree classes 1 through 5) and "No Juniper" as a main effect, location (canopy, intercanopy) as the subplot effects and nutrient treatments as sub-subplot effects in the SAS Institute Inc. (1987) analysis of variance. Mean separation was by the least significant difference (LSD) procedure (Carmer and Swanson 1971).

Results

Analysis of variance showed no significant differences among tree classes (including No Juniper) or for the interaction of tree classes X location (Table 2). The following were significant at $p < 0.005$: location (canopy, intercanopy), bioassay nutrient treatments and the interactions of nutrient treatments X tree class (including No Juniper), location X nutrients, and tree class (including No Juniper) X location X nutrient treatment.

TABLE 2. Analysis of variance (SAS) for bioassay nutrient trial.

Source	df	Probability > F
Site (replications)	4	—
Tree class (TC)	5	.3513
Site x TC	20	—
Location (L)	1	.0049
TC x L	4	.1232
Site x TC x L	20	—
Nutrient treatment (N)	5	.0001
TC x N	20	.0023
L x N	5	.0001
TC x L x N	20	.0052

Comparison of yields between the control and full nutrient treatments averaged among tree classes, "No Juniper" and canopy/intercanopy locations revealed that availability of one or more

nutrients was significantly reduced (Table 3). Average yield for the control treatment for all tree classes, "No Juniper," and soil locations was 1.21 g compared to 5.82 g for the full nutrient treatment. Examination of yields of individual treatments shows that yields of N₀ and S₀ (1.49 and 2.46 g, respectively) were significantly less than those of the full nutrient treatment and, thus, were chiefly responsible for low fertility of these soils as indicated by the control treatment (Table 3). The average yield for the P₀ treatment (5.22 g) was significantly less than that of the full treatment, but the difference was not as substantial as that for N and S. The K₀ and full treatment yields did not differ significantly.

TABLE 3. Barley yields for 6 nutrient treatments averaged across tree classes and locations.

-----Yields (g)-----					
Control	N ₀	P ₀	K ₀	S ₀	Full
1.21 ^E	1.49 ^D	5.22 ^B	5.63 ^A	2.46 ^C	5.82 ^A

Values with the same letter are not significantly different at p < 0.05.

Relative yields (yield of any individual nutrient treatment X₀ divided by the yield of the full nutrient treatment X 100) for N ranged from 19% in soil from "No Juniper" sites to 31% in canopy soil (Table 4). Relative yields for S ranged from

27% in "No Juniper" soil to 58% in canopy soil. By contrast, relative yield for P and K exceeded 83% for all locations.

Because the three-way interaction of tree class X location X nutrient treatment was significant (Table 2), it is appropriate to discuss the source of that interaction at the outset using Table 5. We first compare yields for soils of canopy and intercanopy locations for tree classes 1 through 5. For the control and full treatments, barley yields for canopy and intercanopy locations did not differ among tree classes. Similarity of yields for the full treatment between locations and for all tree classes indicated that the full treatment provided an adequate supply of N, P, K, and S under conditions of this bioassay trial.

TABLE 4. Relative yields 1] (percent) for N, P, K, and S for open, intercanopy, and canopy soils—average of tree classes.

	N	P	K	S
No Juniper	19	95	93	27
Intercanopy	22	83	95	31
Canopy	31	96	99	58

$$1] \text{ Relative yield} = \frac{\text{X}_0 \text{ treatment yield (g)}}{\text{Full nutrient treatment yield (g)}} \times 100$$

Table 5 shows that the N₀ yields did not differ between the two locations for any tree class. This

TABLE 5. Comparisons of barley yields between western juniper canopy (C) and intercanopy (IC) locations for 6 nutrient treatments.

Tree Classes	Treatment											
	Control		N _o		P _o		K _o		S _o		Full	
	-----Location-----											
	C	IC	C	IC	C	IC	C	IC	C	IC	C	IC
	-----g/pot-----											
1	1.141	1.130	1.231	1.136	5.101	5.167	4.383*	5.508	2.375	1.692	5.522	5.341
2	1.242	.878	1.356	1.307	5.438	4.928	6.395	5.54	2.332	1.832	6.029	5.486
3	1.186	.949	1.797	1.364	5.595	5.364	5.899	6.306	2.825	1.793	5.723	6.017
4	1.387	.914	1.473	1.349	6.524*	4.494	5.839	5.722	4.358*	1.684	5.404	6.419
5	1.353	.987	2.023	2.339	4.246	4.523	5.330	5.572	4.417*	2.037	5.488	6.134

LSD = 1.046 for comparison of differences between locations for each tree and nutrient treatment.

* Denotes a significant yield difference (p ≤ 0.05) between canopy and intercanopy soil for an individual tree class and treatment.

LSD = 1.123 for comparisons among tree classes, nutrients, and locations.

suggests that invasion and development of western juniper has had no influence on availability of N. The P_0 barley yields show that P was significantly more available in canopy than intercanopy soil, but only for tree class 4. The response of K was in sharp contrast to that of P. The K_0 yield for canopy soil was significantly less than that for intercanopy soil for tree class 1; for other tree classes, there were no location differences in K supply. The effect of location on S supply was marked; canopy soil was much higher in available S than intercanopy soil for tree classes 4 and 5 (Table 5).

We now compare yields for canopy and intercanopy soils for tree classes 1 through 5 and "No Juniper" areas. This comparison provides an indication of the long-term influence of western juniper invasion and development on availability of individual nutrients in each location. For the in-

tercanopy location, juniper invasion has affected only the supply of P; in the intercanopy soil it was significantly less for tree classes 2, 4, and 5 than for soil from "No Juniper" areas.

Juniper had a greater influence on canopy than on intercanopy soils; differences among tree classes were evident for the P_0 , K_0 , and S_0 treatments (Figure 1). Yields for the P_0 treatment were the same among "No Juniper" through tree class 3, but P supply was significantly higher for soil of tree class 4 than that of tree class 1; P supply for soil of tree class 5 was lower than that of all other tree classes. Yields of the K_0 treatment declined between "No Juniper" and tree class 1 (Table 2) indicating reduced availability with tree establishment. However, K_0 yields then increased and remained constant through tree class 5, indicating that K availability increased after the initial decline. Yields

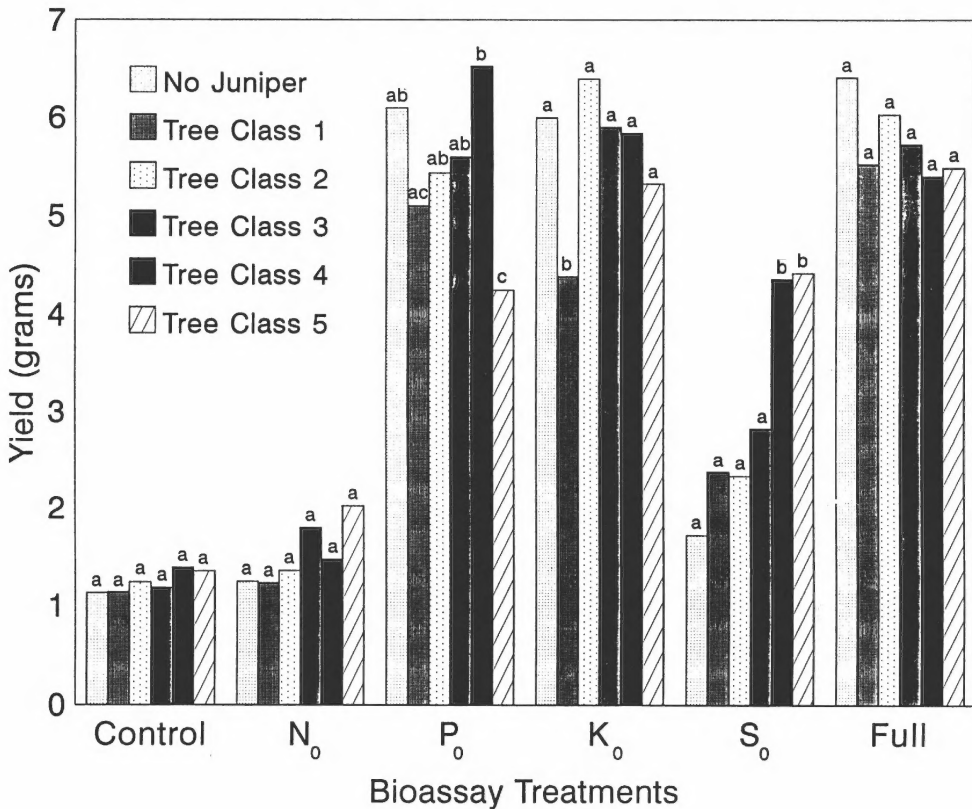


Figure 1. Comparisons of canopy soil barley yields among the 5 tree classes and "No Juniper" for 6 nutrient treatments. Bars with the same letter are not significantly different ($p=0.05$) within an individual treatment. LSD = 1.123

for S were most definitive and showed distinct trends with advancing juniper maturity. There were no differences in S_0 yield between "No Juniper" and the first three tree classes. However, S availability increased markedly for the two older tree classes (Figure 1).

Discussion

The similarity of available N in "No Juniper," intercanopy, and canopy soils was an unexpected result. Most studies of canopy/intercanopy soil nutrient availability have shown differences for available N between canopy and intercanopy locations. In our studies with mesquite (*Prosopis juliflora* Swartz, DC) using the same bioassay technique, available N in soil from beneath tree canopies was 15 times greater than in soil from intercanopy areas (Tiedemann and Klemmedson 1973). Barth (1980) found a 2.4-fold greater nitrate-N concentration in soil under old (540 y) pinyon pine compared to adjacent shrub-dominated areas. Moreover, nitrate-N concentration in soil from beneath pinyon canopies was positively related to tree age from 15 to 540 y. Klopatek (1987) examined available N (NH_4 -N and NO_3 -N) in the 2- to 10-cm soil layer for two sites with mature pinyon-juniper trees 300 to 400 y of age. At one site, the available N was comparable between canopy and intercanopy areas. At another site, available N was 2X greater in soil beneath canopies than in the interspaces. We observed no similar response with increasing tree age.

Differences in N mineralization potential may explain low availability of N in canopy soils of western juniper. Klopatek and Klopatek (1987) provide evidence that nitrifying bacteria are substantially lower in soils beneath canopies of pinyon-juniper trees than intercanopy soil. Possible reasons for low availability of N in canopy soils include leaching of nitrate-N, uptake of available N ions by the fine root system of juniper, high organic C/N ratios, and inhibition of microbial processes by volatile oils from juniper foliage.

The observed similarity of available P in canopy and intercanopy soils (Table 5) for the oldest and largest trees (class 5) presented a contrast to pinyon-juniper woodland studies. These studies (Barth 1980, Everett *et al.* 1986, and Klopatek 1987) indicate improved P availability in soil beneath tree canopies (300 to 540 y old) compared to adjacent interspaces. However, our results do

agree with those of Doescher *et al.* (1987). They found no difference in available P (sodium bicarbonate extractable) in soil beneath canopies of juvenile (<40 y) or mature (>80 y) western juniper compared to interspaces. Average age of class 4 trees, which exhibited greater P availability in canopy than intercanopy soils, was 81 y. Our results suggest there may be a period of time during the development of western juniper between 44 and 135 y that P availability is enhanced in the canopy soil compared to intercanopy soil.

Observed differences in available P between canopy and intercanopy soils (Barth 1980, Klopatek 1987, and Everett *et al.* 1986) for pinyon pine and Utah juniper (*J. utahensis* (Engelm.) Lemmon.) has led to speculation that the lateral root system affects nutrient status of open area soils. There is evidence, including our observations, that juniper roots extend well beyond the canopy edge (Young *et al.* 1984). We found western juniper lateral roots at a distance of 4 canopy radii at a depth of about 30 cm in several sample holes.

Reduced availability of P in intercanopy soils compared to "No Juniper" soils with increasing juniper maturity (tree classes 4 and 5) suggests that lateral roots of western juniper have influenced nutrient capital of the areas between trees. Our results also suggest that the degree of alteration is related to age of western juniper. None of the studies cited above have examined P availability as a function of tree age for intercanopy soils.

Reduced K availability in tree class 1 canopy soils compared to intercanopy soils and "No Juniper" areas (Table 5, Figure 1) may reflect high K demand in young trees for nutrients as they allocate a large part of their resources to roots and foliage (Miller *et al.* 1990).

Results of this study on S supply, especially compared to results for N, are noteworthy. Generally, differences reported in SO_4 -S between canopy and intercanopy soils have been greater than those for NH_4 -N and NO_3 -N. Barth (1980), for example, found 16X and 7.5X more SO_4 -S in the 0- to 10-cm and 10- to 40-cm layers of canopy soil, respectively, than intercanopy soils. By contrast, Barth's canopy soils contained only 2.4X and 4.1X more NO_3 -N at those depths than intercanopy soils. Others (Klopatek 1987, Thran and Everett 1987) have reported NO_3 -N up to 10 times higher in canopy than intercanopy soils. In Klopatek's study, NH_4 -N comprised most of the available N, but the

canopy-intercanopy difference was only about twofold.

Mineralization of soil N and S are in some respects similar and in some respects different (Starkey 1966, McGill and Cole 1981). Nitrogen is mineralized by biological mineralization, whereas S is mineralized by biological and biochemical mineralization processes (McGill and Cole 1981). That S has a dual mineralization system in contrast to the single system for N may help explain the inconsistent relation between N and S mineralization noted by Biederbeck (1978) and the difference in N and S supply noted here. Presumably, biochemical reactions in the S mineralization system would be relatively insensitive to volatile oils present in the canopy environment of this study.

Conclusions

Low P_0 barley yields for intercanopy soils with advancing tree age suggests that the lateral root system of western juniper may have transported significant amounts of P from open areas to the tree and canopy area. This result would seem to support our hypothesis (1) that the lateral root system exploits available nutrients in the intercanopy spaces. Without mass balance data, however, it is uncertain whether reduced P availability in the intercanopy area is a consequence of P export by juniper roots or altered conditions as a consequence of the presence of the lateral roots. Our data from the larger part of this study on mass balance of nutrients should shed light on the question of nutrient transport.

Availability of N and K in soil beneath canopies of western juniper was not greatly enhanced by invasion and development of the tree. Thus, for these nutrients, we reject our hypothesis (2) that nutrient availability beneath the canopy is improved by litterfall accumulation and a microenvironment

improved for accumulation and maintenance of organic matter and nutrients. Phosphorus availability in canopy soil was enhanced for class 4 trees (81 y average age) but then sharply reduced for the oldest tree class (161 y). Sulfur availability was significantly improved in canopy soils with the two oldest tree classes compared to the other tree classes and open soils. Volatile oils in western juniper litter may influence N and S mineralization in several ways, such as to affect net mineralization. However, S availability may be less influenced than N availability because biochemical process reactions are a dominant avenue for production of SO_4 -S.

Relative yields indicate that all locations were N deficient to the point that fertilization may be a viable option for enhancing production of vegetation (Jenny *et al.* 1950). Furthermore, relative yields for S indicate that this nutrient is deficient to the extent that any fertilization should include this element. Moisture is certainly limiting in these habitats, but any management strategy aimed at reducing moisture competition for vegetation production should be coupled with nutrient amelioration.

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Literature Cited

- Baldwin, E. M. 1964. Geology of Oregon. University of Oregon Cooperative Book Store, Eugene. 165 p.
- Barth, R. C. 1980. Influence of pinyon pine on soil chemical and physical properties. *Soil Sci. Soc. Am. J.* 44:112-114.
- Biederbeck, V. O. 1978. Soil organic sulfur and fertility. In: M. Schnitzer and S. U. Khan (eds.). *Soil organic matter. Develop. Soil Sci.* 8:273-310. Elsevier, Amsterdam.
- Bohn, H. L., B. L. McNeal, and G. A. O'Connor. 1979. *Soil Chemistry*. John Wiley and Sons, New York.
- Caraher, D. L. 1978. The spread of western juniper in central Oregon. In: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). *Proceedings of the Western Juniper Ecology and Management Workshop*; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 3-7.

- Carmer, S. G., and M. R. Swanson. 1971. Detection of differences between means: a Monte Carlo study of five pairwise multiple comparison procedures. *Agron. J.* 36:40-945.
- Dealy, E. J., J. M. Geist, and R. S. Driscoll. 1978. Communities of western juniper in the intermountain Northwest. *In: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 11-29.*
- Doescher, P. S., L. E. Eddleman, and M. R. Valtkus. 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. *Northwest Sci.* 61:97-102.
- Driscoll, R. S. 1964. Vegetation-soil units in the central Oregon juniper zone. *USDA For. Serv. Res. Pap. PNW-19. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. 60 p.*
- Eddleman, L. E. 1987. Western juniper in central Oregon. *In: R. L. Everett, (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 255-259.*
- Everett, R. L., S. H. Sharrow, and D. F. Thran. 1986. Soil nutrient distribution under and adjacent singleleaf pinyon crowns. *Soil Sci. Soc. Am. J.* 50:788-792.
- Garcia-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert shrub community. *Ecology* 51:81-88.
- Jenny, H. 1930. A study of the influence of climate upon nitrogen and organic matter content of the soil. *Missouri Agric. Exp. Sta. Res. Bull.* 152.
- . 1961. Derivation of state factor equations of soils and ecosystems. *Soil Sci. Soc. Am. Proc.* 25:385-388.
- Jenny, H., J. Vlamis, and W. E. Martin. 1950. Greenhouse assay of fertility of California soils. *Hilgardia* 20:1-8.
- Klemmedson, J. O. 1983. State of dry matter and nutrients in soil-plant systems of Arizona fescue and mountain mahogany. *J. Range Manage.* 36:558-564.
- Klopatek, C. C., and J. M. Klopatek. 1987. Mycorrhizae, microbes, and nutrient cycling processes in pinyon-juniper ecosystems. *In: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 360-364.*
- Klopatek, J. M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. *Soil Sci. Soc. Am. J.* 51:453-457.
- Major, J. 1951. A functional, factorial approach to plant ecology. *Ecology* 32:392-412.
- Martin, R. E. 1978. Fire manipulation and effects in western juniper (*Juniperus occidentalis* Hook.). *In: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 121-136.*
- McGill, W. B., and C. V. Cole. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. *Geoderma* 26:267-286.
- Miller, P. M., L. E. Eddleman, and S. Kramer. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. *Forest Sci.* 36:734-747.
- SAS Institute Inc. 1987. SAS/STAT Guide for personal computers, version 6 ed., Gary, NC.
- Starkey, R. L. 1966. Oxidation and reduction of sulfur compounds in soils. *Soil Sci.* 101:297-306.
- Thran, D. F., and R. L. Everett. 1987. Soil nutrient changes following tree harvest. *In: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 387-390.*
- Tiedemann, A. R. 1987. Nutrient accumulations in pinyon-juniper ecosystems—managing for future site productivity. *In: R. L. Everett (compiler). Proceedings, Pinyon-Juniper Conference; 13-16 Jan. 1986; Reno, Nevada. USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Res. Sta., Ogden, Utah. Pp. 352-359.*
- Tiedemann, A. R., and J. O. Klemmedson. 1973. Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. *Soil Sci. Soc. Am. Proc.* 37:107-111.
- . 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Sci. Soc. Am. J.* 50:472-475.
- United States Department of Commerce. National Oceanic and Atmospheric Administration. 1973. Climatological Data, Oregon, Annual Summary 79 (13):1-9.
- United States Department of Agriculture, Soil Conservation Service. 1986. General Soil Map, State of Oregon. General Soils 4-R-39694. USDA Soil Conservation Service, Forest Service, and United States Department of the Interior, Bureau of Land Management. One page map.
- Winegar, H., and W. Elmore. 1978. Mechanical manipulation of western juniper—some methods and results. *In: R. E. Martin, J. E. Dealy, and D. L. Caraher (eds.). Proceedings of the Western Juniper Ecology and Management Workshop; Bend, Oregon; January 1977. USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. Pp. 107-119.*
- Young, J. A., R. A. Evans, and D. A. Easi. 1984. Stem flow on western Juniper (*Juniperus occidentalis*) trees. *Weed Sci.* 32:320-327.

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Robert J. Anderson, Weyerhaeuser Company, Technology Center, Tacoma, Washington 98477

Elk (*Cervus elaphus roosevelti*) Dietary Composition and Quality in the Mount St. Helens Blast Zone

Abstract

We compared diet composition and diet quality of elk using the Mount St. Helens "blast zone" in 1985 to elk populations in more forested areas in the Pacific Northwest. Fecal analysis indicated that elk at Mount St. Helens consumed more forbs during summer (46-65% density of fecal fragments), more grasses during fall (38-62%), less ferns (< 3%), and in some cases less browse (20-42%), than has been reported for most west coast elk populations. Early successional forbs such as fireweed (*Epilobium angustifolium*), pearly everlasting (*Anaphalis margaritacea*), catsear (*Hypochaeris radicata*), mesic community species such as horsetail equisetum (*Equisetum* spp.) and willow (*Salix* spp.), and pasture grasses such as red fescue (*Festuca rubra*) and ryegrasses (*Lolium* spp.) that were seeded after the eruption were dominate in the feces of Mount St. Helens elk. Levels of *in vitro* dry matter digestibility in the diets of Mount St. Helens elk were higher and crude protein equal or lower than in diets of elk inhabiting managed and old-growth forests elsewhere in the Pacific Northwest. We hypothesize that because of nutritional differences in diets, elk inhabiting primarily old-growth forests will have a lower mean fecundity and higher mortality rate than elk inhabiting managed forests at the same elk densities. However, because structural characteristics of old-growth forests buffer elk from high travel costs and reduced forage availability during periodic heavy, wet snows, we hypothesize that vital rates will be less variable.

Introduction

Large-scale conversion of old-growth forests to even-aged, regenerating forests has caused concern over the loss of old-growth forests to west coast cervid populations (Smithey *et al.* 1985, Raedeke and Lemkuhl 1985). Benefits of old-growth forests to deer (*Odocoileus hemionus*) and elk have been attributed to 3 forest characteristics: (1) overstory structure that intercepts a substantial amount of snow, yet has sufficient openings to let sunlight reach the forest floor and promote understory development (Bunnell and Jones 1984, Hanley and Rose 1987), (2) abundance of arboreal lichens as a source of forage (Stevenson and Rochelle 1984), and (3) value as thermal cover (Schoen *et al.* 1984, Zahn 1985). The importance of old-growth forest characteristics to cervid species varies seasonally and across geographic areas depending on climatic regimes and characteristics of other habitats (Hanley *et al.* 1984). Where snow accumulates in winter, as in southeast Alaska, deer may require old-growth forests for energy conservation and foraging areas (Bunnell and Jones 1984, Hanley

1984). Further south, where snow is less persistent, a wider array of silvicultural options may exist for maintaining or enhancing cervid populations.

Understanding constraints on elk foraging behavior (Merrill 1994), and the nutritional adequacy of diets obtained from different forest types and seral stages are important prerequisites for evaluating management options for cervids. Elk in west coast forests show a high degree of dietary plasticity (Jenkins and Starkey 1991), which may affect nutrition and population dynamics. Diet composition and quality of elk populations have been examined in old-growth forests (Leslie *et al.* 1984, Leslie *et al.* 1987) and managed forests where several seral stages existed in proximity (Hanley 1984, Janz 1983). In this paper, we describe summer-fall composition and quality of diets of elk which inhabited the early successional forests that developed after the eruption of Mount St. Helens, and compare them to similar dietary studies on elk inhabiting later stages of forest succession in the Pacific Northwest.

Study Area

In 1985, we studied diet composition of elk inhabiting the northwestern portion of the Mount St. Helens "blast zone" in southwestern Washington within the Green River and North Fork of the Toutle River drainages. Elk reinvaded this area shortly

¹Present address: College of Natural Resources, University of Wisconsin, Stevens Point, WI 54481

²Box 132, Toutle, WA 98649

³Wildlife Biology Department, School of Forestry, University of Montana, Missoula, MT 59812

after the eruption in 1980 and by 1985 helicopter surveys indicated summer elk densities were $1.8 \pm 0.20/\text{km}^2$ ($\bar{x} \pm \text{s.e.}$) (Merrill 1987).

The Mount St. Helens area is included in the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973), although tree plantations prior to the eruption and adjacent to the blast zone were predominantly Douglas-fir (*Pseudotsuga menziesii*). Vegetative response in the 60,000 ha blast zone varied across the landscape depending on type of disturbance (e.g. pyroclastic flow, mudflow, blow-down, scorched), pre-eruption stand age, the presence of snow at the time of eruption, depth of tephra deposition, and post-eruption treatments (e.g. seeding, tree salvage operations, burning, bulldozing) (Means *et al.* 1982, papers in Bilderback 1987, Halpern *et al.* 1990). Because ash accumulation was relatively low, and salvage logging and site preparation mixed ash and soils, vegetation recovery in the northwestern portion of the blast zone was rapid.

Five early successional plant communities were identified based on species canopy coverage (Merrill 1987). The fireweed/pearly everlasting community made up the largest part of the study area (45%) and was dominated by catsear, groundsel (*Senecio sylvaticus*, *S. jacobaea*), thistle (*Cirsium arvense*), velvet grass (*Holcus lanatus*), blackberries (*Rubus ursinus*, *R. spectabilis*), and mahonia (*Berberis nervosa*). The fireweed/ glacier lily (*Erythronium grandiflorum*) community (4%) occurred at high elevations where ash accumulation was generally > 12 cm. Many of the same species occurred in this community as in the fireweed/pearly everlasting community, but canopy coverage was not as great, and several mesic-site species such as huckleberry, (*Vaccinium membranaceum*), dogwood (*Cornus canadensis*), and glacier lily were relatively abundant. The fireweed/red fescue community (20%) dominated sites that were young clearcuts (< 2 yrs) prior to the eruption and were aerially seeded after the eruption with a grass-clover mixture (e.g. *Lolium perenne*, *L. multiflorum*, *Festuca rubra*, *Trifolium pratense*, *T. repens*). The red fescue/clover (*Trifolium* spp.) community (14%) occurred only on the western portion of the debris avalanche of the North Fork Toutle River. Wet seep areas ($< 1\%$) were dominated by horsetail equisetum, rushes (*Juncus* spp.), montia (*Montia siberica*), and willow and were scattered throughout the study area. Forests adjacent to the blast zone (16%) were owned primarily by the

Weyerhaeuser Company. Douglas-fir was the primary tree species grown and site productivity was moderately high (Stevens *et al.* 1987).

Topography of the area is mountainous with elevations ranging from 240 m to about 1200 m. The climate is Pacific maritime with wet, mild winters and cool, dry summers. Annual precipitation is 225 cm/yr, occurring predominantly from November to April. Mean daily temperatures averaged 23°C in July.

Methods

Food habits of elk were determined using micro-histological identification of plant fragments in the feces of elk. Fresh fecal pellets were collected at elk feeding sites across the study area in June through November 1985. Five pellets from each of 50 groups were composited by month except for November when only 34 pellet groups were collected. Pellets were dried at 50°C for 48 hours. Each composite sample was ground and mixed in a Wiley mill to pass through a 0.1 mm screen.

Twenty slides of fecal plant fragments were prepared for each monthly fecal sample and 20 fields of view were read per slide. The amount each food item contributed to a sample (slide) was quantified using the frequency of occurrence of the species (Sparks and Malechek 1968). Frequencies were then converted to density estimates (Fracker and Brischle 1944).

Herbaceous plants comprising > 1 percent of the feces were collected and analyzed for percent nitrogen and *in vitro* digestibility when plants were in three phenological growth stages. Forbs were collected when they were vegetative, late vegetative-early flowering, and fruiting/mature. Grasses were collected when they were vegetative, flowering/fruiting, and senescent/cured. Species collections were made from at least 5 different plants at 5 sites and plant material combined. Only up to the terminal 10 cm of a plant was collected and plant parts were collected in the proportion they occurred on the terminal portion of a plant.

To approximate the nutritive value of herbaceous species eaten by elk each month, we used the value of the modal phenological stage of each species monitored at 10 sites. Two of the sites were at high elevation (> 900 m) and 8 at low elevation (≤ 900 m), which corresponded to the approximate distribution of observations of radio-collared elk (82% < 900 m, $n = 15$ elk) during the summer of 1984

(Merrill 1987). Predominate phenological stage at each site was determined by visually inspecting up to 50 arbitrarily chosen plants of each species. When we did not collect species eaten by elk at the modal phenology for nutritive analysis ($n = 15$ during the 6 months), and for unknown species within a forage category, we used the average nutrient value of all species in a forage class for the month.

Browse species were collected in early July to represent nutritive values of browse species in June and July, and in late August-early September to represent nutritive values in August and September. Composited shrub collections consisted of up to 10 cm of the terminal new growth of at least 20 different individuals of the major shrub species from 4 different sites. Leaves and stems were collected in proportion to their occurrence. In contrast, only new growth of twigs was collected in late October to represent nutritive values of browse in October and November because leaf drop was almost complete by mid-October.

All plants were dried at 50°C for 48 hours. Forage species were analyzed for nitrogen (N) using macro-kjeldahl techniques and for *in vitro* dry matter digestibility (IVDMD) following methods of Tilley and Terry (1963). A ruminally fistulated elk maintained on an alfalfa diet was used as the source of inoculum for IVDMD determinations.

The quality of a monthly diet was simulated following the procedure presented by Westoby (1974) and used by Leslie *et al.* (1984) and Janz (1983). Diet quality was the average monthly nutrient content of forages weighted by the proportion a forage occurred in the feces.

Differences in monthly fecal composition were compared by forage class using Tukey's HSD multiple comparison test. Percentage values were transformed using an arcsine-square root transformation prior to analysis (Sokal and Rohlf 1981). Seasonal trends in diet quality were examined using a Spearman rank correlation (r_s) (Siegel 1956). Differences in nitrogen and IVDMD between phenological stages were tested using paired t-tests by species within a forage class.

Results

Fecal Analysis

Forbs were dominate in the feces of elk from June through August, but declined in importance from September through November (Table 1). Five

forb species, including horsetail equisetum, catsear, pearly everlasting, fireweed, and clover, comprised 47-75 percent of the forb component of feces during summer. Graminoids in the feces comprised >60 percent in November. Grass species that were aerially seeded after the eruption to prevent ash erosion and to control dust, including red fescue, tall fescue (*Festuca arundinacea*), and annual rye grasses, were the dominant grass species in the fall fecal samples. Shrub use peaked in September, but comprised >20 percent of feces during all months. Willows, elderberry (*Sambucus racemosa*, *S. cerulea*), salmonberry (*Rubus spectabilis*), and huckleberry (*Vaccinium* spp.) consistently made up the greatest proportion of the shrubs found in the feces each month. Ferns comprised a consistently low proportion of the fecal samples.

Forage and Diet Quality

Quality of simulated elk diets was highest early in the growing season and declined as the season progressed ($r_s = 1.0$, $n = 6$, $P = 0.01$) (Table 2). By June, many grasses were already in flowering stage and had declined in forage quality. In contrast, most forbs consumed by elk in June were still in early stages of plant growth. IVDMD declined significantly in forbs and grasses with plant maturity (Table 3). Nitrogen declined rapidly in grasses and forbs between the vegetative stage and flowering stage (Table 3), but, thereafter, N decline in forbs was not significant ($t = 2.39$, $df = 4$, $P = 0.08$). Fern and conifer species were generally lower in IVDMD and N than other forage classes (Table 4). Nutritive values of shrubs declined significantly from summer to fall, but were high in N in fall compared to cured grasses.

Discussion

Mount St. Helens elk consumed more forbs during summer, more grasses during fall, less ferns, and in some cases less browse, than has been reported for most west coast elk populations (see Jenkins and Starkey 1991 for review). Differences in food habits among elk populations are probably due to broad-scale differences in the availability of different forage classes, since availability of forage classes (herbs, ferns, shrubs, conifers) is a predictable function of forest succession (Issac 1940, Long and Turner 1975, Harestad 1979, Witmer *et al.* 1985). Diets of elk at Mount St. Helens were dominated by forbs in summer and grasses in fall. Greater

TABLE 1. Mean percent density of plant fragments identified in elk feces collected in the northwestern portion of the Mount St. Helens blast zone during summer and fall of 1985.

	June	July	Aug	Sept	Oct	Nov
GRAMINOIDS						
<i>Agrostis</i> spp.	2.4	0.5	0.3	0.6	2.2	2.2
<i>Bromus</i> spp.	0.1	0.0	0.1	0.2	0.4	2.1
<i>Carex</i> spp.	2.2	1.6	0.4	0.5	0.7	1.6
<i>Dactylis glomerata</i>	0.1	0.5	0.3	0.3	2.4	4.3
<i>Deschampsia elongata</i>	0.7	0.0	0.3	0.6	1.3	1.1
<i>Elymus glaucus</i>	1.3	0.7	1.6	2.0	3.5	3.0
<i>Festuca arundinacea</i>	0.5	0.3	0.8	2.2	3.4	8.0
<i>Festuca rubra</i>	2.2	0.9	2.4	5.9	5.8	18.4
<i>Holcus lanatus</i>	2.0	1.2	2.0	2.2	3.8	5.1
<i>Juncus</i> spp.	0.8	0.8	0.1	0.2	0.5	0.4
<i>Lolium</i> spp.	1.5	0.2	0.2	1.8	6.0	6.7
<i>Luzula divaricata</i>	0.1	0.2	0.3	1.5	0.8	0.4
<i>Phleum pratense</i>	0.2	0.3	0.4	0.9	1.4	3.4
<i>Poa</i> spp.	0.1	0.1	0.8	0.8	1.5	0.4
Unidentifiable grasses	3.3	1.7	2.8	6.1	4.6	5.2
Total graminoids	17.5b	8.8a	12.8ab	25.8c	38.3d	62.3e
FERNS						
<i>Blechnum spicant</i>	1.2	0.2	0.2	0.0	0.2	0.6
<i>Lycopodium</i> sp.	0.1	0.1	0.1	0.0	0.3	0.1
<i>Polystichum munitum</i>	0.0	0.4	0.2	0.2	0.1	1.0
<i>Pteridium aquilinum</i>	1.3	0.8	0.0	0.2	0.3	0.6
Total ferns	2.6b	1.5ab	0.5a	0.4a	0.9a	2.3ab
FORBS						
<i>Achillea millefolia</i>	0.8	0.2	0.1	0.0	0.1	0.0
<i>Anaphalis margaritaceae</i>	1.5	5.0	3.1	1.1	0.1	0.2
<i>Arnica montana</i>	0.1	0.0	0.0	0.0	0.0	0.0
<i>Dicentra formosa</i>	0.2	3.4	0.3	0.2	0.1	0.0
<i>Epilobium angustifolium</i>	0.2	8.2	28.5	4.2	4.5	1.2
<i>Epilobium glaberrimum</i>	1.0	2.7	0.5	0.0	0.0	0.0
<i>Equisetum</i> spp.	10.5	10.7	8.2	5.0	3.0	2.3
<i>Galium boreale</i>	0.1	0.0	0.0	0.0	0.0	0.0
<i>Hieracium albiflora</i>	0.1	0.1	0.0	0.0	0.0	0.0
<i>Hypochaeris radicata</i>	8.3	13.1	3.6	1.8	2.4	0.9
<i>Lotus corniculatus</i>	0.0	0.7	0.4	0.5	0.1	0.3
<i>Lysichiton americana</i>	0.2	0.0	0.1	0.0	0.0	0.0
<i>Lupinus</i> spp.	1.0	0.2	0.1	1.3	1.5	1.3
<i>Maianthemum dilatatum</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mimulus guttatus</i>	0.8	0.4	0.5	0.1	0.0	0.0
<i>Montia siberica</i>	0.0	0.8	0.1	0.1	0.1	0.0
<i>Oxalis oregana</i>	0.3	0.1	0.0	0.0	1.6	0.6
<i>Plantago lanceolata</i>	0.3	0.2	0.0	0.0	0.0	0.1

continued, next page

Table 1, continued

	June	July	Aug	Sept	Oct	Nov
<i>Petasites frigidus</i>	0.0	0.0	0.0	0.2	0.0	0.0
<i>Ranunculus radicata</i>	0.5	0.1	0.0	0.0	0.0	0.0
<i>Stachys cooleyae</i>	0.0	1.1	0.3	0.0	0.0	0.1
<i>Trifolium</i> spp.	4.6	2.5	3.3	7.1	4.0	2.5
<i>Typha latifolia</i>	0.1	1.3	0.7	0.5	0.0	0.0
<i>Veronica officinale</i>	0.2	0.1	0.0	0.0	0.0	0.2
Unidentifiable forbs	15.4	14.6	12.2	9.6	6.1	5.3
Total forbs	46.2c	65.5d	62.1d	31.7b	23.6b	15.0a
SHRUBS AND TREES						
<i>Acer circinatum</i>	1.9	0.0	0.3	0.7	0.2	0.8
<i>Acer macrophyllum</i>	0.9	0.4	0.7	0.6	0.2	0.3
<i>Alnus rubra</i>	0.7	0.2	0.1	0.9	0.6	0.1
<i>Berberis nervosa</i>	0.3	0.1	0.0	0.2	0.1	0.1
<i>Gaultheria shallon</i>	0.1	0.2	0.5	0.9	1.0	0.2
<i>Populus trichocarpa</i>	0.1	0.6	0.6	0.6	1.2	0.9
<i>Pseudotsuga menziesii</i>	2.0	0.0	0.1	0.2	0.1	0.1
<i>Ribes bracteosum</i>	0.0	0.1	0.0	0.0	0.0	0.0
<i>Rosa nutkana</i>	0.5	0.3	0.2	0.9	0.9	0.1
<i>Rubus ideaus</i>	0.9	0.3	0.1	0.6	0.1	0.0
<i>Rubus parviflorus</i>	0.1	0.1	0.4	0.2	1.2	0.8
<i>Rubus spectabilis</i>	3.1	1.2	1.3	3.4	2.3	0.9
<i>Rubus ursinus</i>	0.5	0.0	0.0	0.5	0.6	0.1
<i>Salix</i> spp.	15.6	15.1	14.0	21.5	18.1	5.8
<i>Sambucus racemosa</i>	1.5	2.1	1.4	2.1	2.2	1.8
<i>Tsuga heterophylla</i>	0.2	0.1	0.1	0.0	0.1	0.0
<i>Vaccinium</i> spp.	0.8	0.0	0.4	1.7	1.4	0.7
Unidentifiable shrubs	4.5	3.4	4.4	7.1	6.9	7.4
Total shrubs and trees	33.7bc	24.2ab	24.6ab	42.1c	37.2bc	20.4a
TOTAL	100	100	100	100	100	100

TABLE 2. Dietary levels of *in vitro* dry matter digestibility (%) and crude protein (% nitrogen x 6.25) for elk in the Mount St. Helens blast zone during the summer and fall of 1985.

Month	Digestibility	Crude Protein
June	61.8	15.6
July	57.8	14.7
August	52.2	12.3
September	47.2	9.8
October	45.5	8.9
November	44.2	7.1

than 85 percent of the composite home range of elk at Mount St. Helens was in early seral stages of forest succession. Standing herbaceous biomass averaged 1145 kg/ha in July in the early successional communities with forbs, grasses, and ferns comprising 63 percent, 26 percent, and 11 percent of the standing biomass, respectively (Merrill 1987). Grasses seeded after the eruption were conspicuous in about 34 percent of the composite home range of elk (20% on the debris avalanche which elk used only in fall and winter), while the remaining early successional communities (45%) could not

TABLE 3. Percent *in vitro* dry matter digestibility (IVDMD) and percent nitrogen (N) of major herbaceous forages collected by phenological stage from seral communities in the northwestern portion of the Mount St. Helens blast zone during the summer and fall of 1985.

	Vegetative		Flowering		Mature	
	IVDMD	N	IVDMD	N	IVDMD	N
GRAMINOIDS						
<i>Agrostis</i> spp.			58.3	1.34	35.9	0.54
<i>Carex</i> spp.	75.4	2.60	63.3	1.94	30.7	0.75
<i>Dactylis glomerata</i>	71.3	3.37	41.6	1.19		
<i>Deschampsia elongata</i>			58.8		36.1	
<i>Elymus glaucus</i>	71.1	3.75	64.8	1.40	46.9	0.84
<i>Festuca arundinaceae</i>	75.2	1.46	55.2	1.60	42.3	0.61
<i>Festuca rubra</i>	63.5	2.33	51.5	1.17	28.0	1.05
<i>Holcus lanatas</i>	80.8	2.56	64.9	2.18	53.7	1.65
<i>Lolium perenne</i>			62.3	1.09	39.9	0.76
<i>Luzula divaricata</i>			39.0	1.15	39.8	1.03
<i>Phleum pratense</i>			74.5	1.85		
<i>Poa</i> sp.			55.7	1.75	53.2	1.09
Mean ¹	72.8 ^a	2.63 ^a	57.5 ^b	1.52 ^a	40.7 ^c	0.92 ^c
FORBS						
<i>Anaphalis margaritacea</i>	68.5	2.57	57.3	2.32	43.3	1.79
<i>Dicentra formosa</i>			66.8	2.98		
<i>Epilobium angustifolium</i>	60.0	4.10	57.5	2.48	43.4	1.13
<i>Epilobium glaberrimum</i>	62.4	3.74	44.8	2.42	34.4	1.68
<i>Equisetum</i> spp.	65.5	2.28	50.7	1.43		
<i>Hypochaeris radicata</i>	75.0	1.77	69.4	1.63	63.9	1.30
<i>Lupinus</i> spp.	81.1	3.30	73.8	2.86	58.3	2.32
<i>Maianthemum dilatatum</i>	71.0					
<i>Mimulus guttatus</i>	73.6					
<i>Oxalis oregana</i>	86.9	2.06				
<i>Plantago lanceolata</i>	61.2		52.4	1.51		
<i>Ranunculus radicata</i>	66.8	2.75				
<i>Stachys cooleyae</i>	66.6		63.9	1.66		
<i>Trifolium</i> spp.	86.4	4.16	70.1	3.07	68.0	3.17
<i>Typha latifolia</i>	52.0	2.95	59.2	2.93		
<i>Veronica officinale</i>			62.1	1.78		
Mean	70.0 ^a	3.10 ^a	61.1 ^b	2.29 ^b	51.8 ^c	1.92 ^b

¹ Different superscripts indicate significant differences in IVDMD or N between phenological stages (vegetative vs. flowering, flowering vs. mature) within a forage class, paired t-test, $P \leq 0.05$.

be distinguished floristically from adjacent clear cuts outside the blast zone (Merrill 1987).

In contrast, analyses of elk feces collected in the Hoh Valley on the Olympic Peninsula of Washington (Leslie *et al.* 1984) indicated that elk diets were higher in ferns and conifers (23%) and lower in

forbs (37%) in summer, and lower in grasses in fall (17-26%) than elk feces at Mount St. Helens. Sixty-five percent of the composite home range used by elk in the Hoh Valley consisted of old-growth forests with understories dominated by swordfern, huckleberries, and mosses (Leslie *et al.* 1984). Early

TABLE 4. Percent *in vitro* dry matter digestibility (IVDMD), and percent nitrogen content (N) of up to the terminal 10 cm of new twigs and leaves of ferns and shrubs collected in early July and late August–early September, and of new twigs collected in late October in 1985 in the northwestern portion of the Mount St. Helens blast zone.

	July		September		October	
	IVDMD	N	IVDMD	N	IVDMD	N
FERNS						
<i>Blechnum spicant</i>	31.8	1.20	24.4	1.56	29.9	1.43
<i>Polystichum munitum</i>	26.2	3.38	20.7	2.22	20.0	1.55
<i>Pteridium aquilinum</i>	42.3	3.27	21.6	1.72	16.1	1.83
Mean	33.4	2.62	22.2	1.83	22.0	1.60
SHRUBS						
<i>Acer circinatum</i>	63.7	1.56	49.5	1.33	26.5 ¹	1.21
<i>Acer macrophyllum</i>	50.1	1.78	40.8			
<i>Alnus rubra</i>	49.6	2.70	37.2			
<i>Berberis nervosa</i>	64.7	1.83	38.9	1.10		
<i>Gaultheria shallon</i>	21.8	0.90	22.4	0.78		
<i>Populus trichocarpa</i>	60.2	3.19	56.1	1.68		
<i>Rubus ideaus</i>	44.8	2.24	46.9	1.72		
<i>Rubus parviflorus</i>	54.2	1.60	49.4	1.45	41.0	1.31
<i>Rubus spectabilis</i>	48.5	3.03	21.8	1.63	20.5	1.33
<i>Rubus ursinus</i>	54.0	1.78	40.2	1.53		
<i>Salix</i> spp.	46.5	2.83	34.1	1.60	27.7	1.61
<i>Sambucus racemosa</i>	68.3	3.01	58.6	1.92	48.0	1.20
<i>Vaccinium</i> spp.	58.7	2.90	48.7	1.80	39.9	1.38
Mean	52.7 ^a	2.25 ^{a 1}	41.9 ^b	1.50 ^b	33.9 ^c	1.34 ^c
CONIFERS						
<i>Pseudotsuga menziesii</i>	34.2	1.60	32.5	1.50	31.3	1.51
<i>Tsuga heterophylla</i>	30.3	1.30	27.0	1.36	25.7	1.33
Mean	32.3	1.45	29.8	1.43	28.5	1.40

¹ Different superscripts indicate significant differences in IVDMD or N between collection dates (July vs. September, September vs. October) within a forage class, paired t-test, $P \leq 0.05$.

successional forests were comparatively rare and grasses and forbs were primarily restricted to deciduous communities (e.g. big leaf maple, cottonwood, and alder communities) and areas along floodplains (Leslie *et al.* 1987). Both shrub abundance (4–47 kg/ha, Leslie 1983:Table 9) and the occurrence of shrubs (9%) in elk feces (Leslie *et al.* 1984) were low in the Hoh Valley. Heavy browsing by a high density, unhunted elk population have been reported for this area (Schwartz and Mitchell 1945, Jenkins and Starkey 1980, Leslie *et al.* 1987).

In managed forests of Vancouver Is., B.C. and western Oregon and Washington, where early and late successional stages were interspersed, fecal analysis indicated that diets of elk were also lower

in forbs (2–38%) in summer and grasses (4–38%) in fall than in elk diets at Mount St. Helens, but higher in shrubs (25–60%) (Janz 1983, Hanley 1984).

Fecal analysis presented here represent food consumed during only one summer and annual variation in diets is likely to occur. However, preliminary analysis of elk feces collected in the same area in May (grasses: 25%; forbs: 53%; shrubs: 15%; ferns: 4%; conifers: 3%) and November (grasses: 73%; forbs: 16%; shrubs: 6%; ferns: 4%; conifers: 1%) of 1982 (Merrill, unpublished data) indicated that the patterns we observed in 1985 were consistent among years. Snow was ephemeral in the 5 years following the eruption at the elevations where

elk spent fall and winter at Mount St. Helens and was not considered important in habitat selection (Merrill 1987) or probably diet selection (Merrill 1994).

Determination of diets from plant fragments in feces, also can be biased by differential digestibility of ingested plant species (Dearden *et al.* 1975, Vavra and Holechek 1980, Holechek *et al.* 1982, Gill *et al.* 1983, Alipayo *et al.* 1992). Analyses of feces from elk inhabiting Mount St. Helens were not corrected for these potential biases, but based on corrections for common west coast species (Leslie *et al.* 1983) the high proportion of forbs and low proportion of ferns and conifers in the feces of Mount St. Helens elk are likely to reflect conservative trends in the diet.

Differences in food habits may have important implications for the quality of diets of west coast elk populations. Dry matter digestibility of simulated diets of elk at Mount St. Helens were about 30 percent higher in summer, and 25 percent higher in fall than has been reported for elk inhabiting old-growth forests in Olympic National Park, Washington (summer 41%, fall 37-40%; Leslie *et al.* 1984) and elk inhabiting managed forests on Vancouver Island, B.C. (summer 42%, fall 35%; Janz 1983). Differences were largely due to the high proportion of forbs consumed by elk at Mount St. Helens. Forbs, relative to evergreen ferns and conifers are high in IVDMD (Rochelle 1980, Leslie *et al.* 1984, Janz 1983, this study). Additionally, because cell walls of forbs are thin, they can be broken down and passed rapidly (Spalinger *et al.* 1986), thus permitting high total intake.

In contrast to IVDMD, crude protein levels of simulated elk diets at Mount St. Helens appeared to be equal or below those reported for other west coast areas (Leslie *et al.* 1984: summer 15.9%, fall 13.4%; Janz 1983: summer 15.3%, fall 9.9%). Particularly low levels of crude protein in simulated fall diets of Mount St. Helens elk were due to a high consumption of grasses (26 to 62%). Nonetheless, dietary crude protein in all studies exceeded the generally accepted 5-7 percent needed for meeting metabolic fecal losses (Mould and Robbins 1981), but were lower than the 20 percent needed for maximum weight gain by white-tailed deer fawns (Ullrey *et al.* 1967).

Because secondary plant compounds, such as tannins, reduce protein availability and digestibility of cell solubles, their concentrations may alter

the relative value of diet quality among areas. Only a few studies have quantified concentrations of tannins in west coast forages (Hanley *et al.* 1987, Happe *et al.* 1990, Hanley *et al.* 1992). If tannin levels are higher in forbs than other forage classes (Robbins *et al.* 1987a, Robbins *et al.* 1987b, Hanley *et al.* 1992), particularly when growing in the open (Hanley *et al.* 1987), the potential energy and protein in the diets of Mount St. Helens elk may be much lower than our data indicate. However, salivary proteins of elk may be similar to deer and reduce the effects of tannins by forming soluble complexes which are stable throughout the digestive tract (McArthur *et al.* 1991).

The above comparisons of food habits and dietary quality are tentative because of the short-term nature of the studies (≤ 2 years) and because of differences in sampling procedures and other characteristics of the study areas. For example, although the Mount St. Helens, Hoh Valley, and Vancouver Island study sites fall primarily within the western hemlock bioclimatic zone, differences in soils and total rainfall (Hoh Valley > Vancouver Island $\geq$ Mount St. Helens) are likely to influence the relative abundance of specific habitat types, which differ in species composition and potential forage value (Nyberg and Janz 1990). Nonetheless, we believe the data are sufficient to hypothesize that summer-fall nutrition of elk varies with the dominant pattern of forest succession in a landscape. In landscapes of primarily early successional stages, forbs and deciduous browse species are abundant and provide high energy intake because they are high in cell solubles, and have rapid passage rates. In contrast, areas dominated by ferns, evergreen shrubs, and conifers, as found in old-growth forests, may provide low energy intake, but adequate protein.

In fall, and in winter (Jenkins and Starkey 1993), availability of grasses to west coast elk can provide an important source of energy. Graminoids are typically more abundant in early seral communities than in closed canopied and old-growth forests (Harestad 1979, Hanley 1984, Leslie 1983, Merrill 1987). High standing crops of grasses, however, are limited primarily to disturbed sites, such as flood plains (Jenkins and Starkey 1980, Leslie *et al.* 1984), lowland wet meadows (Paige 1990), and seeded clearcuts (Becker 1989), since most natural grasslands in the west coast have been encroached by human settlement (Raedeke and Taber 1982).

Our arguments do not negate the importance of old-growth forests to elk in west coast environments. Instead, we hypothesize that elk populations living within landscapes dominated by different forest stages may have different population responses to environmental conditions as a result of distinctive nutritional regimes. If elk populations inhabiting primarily old-growth forests are more energy-limited relative to elk populations in naturally diverse or managed forests, particularly where grass seeding is a common practice, we hypothesize that they will have lower mean fecundity and higher mortality rates at the same elk densities. However, we hypothesize that these rates will be less variable than in managed forests because structural characteristics of old-growth forests buffer elk from high costs of travel and from reduced forage availability during periodic heavy, wet snows in winter. The limited

data available on long-term dynamics of elk populations in pastures and forests systems in western Oregon are consistent with these hypotheses (Taylor 1986). We encourage future studies to address the effects of forest dominance and diversity on population processes of elk.

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Literature Cited

- Alipayo, D., R. Valdez, J. L. Holechek, and M. Cardenas. 1992. Evaluation of microhistological analysis for determining ruminant diet botanical composition. *J. Range Manage.* 45:148-152.
- Becker, J. M. 1989. Forage enhancement in the Pacific Northwest: improving elk habitat and forest regeneration. Univ. of Washington, Seattle. M.S. Thesis.
- Bilderback, D. E. 1987. Mount St. Helens 1980: botanical consequences of the explosive eruptions. Univ. Calif. Press, Berkeley.
- Bunnell, F. L., and G. W. Jones. 1984. Black-tailed deer and old-growth forests—a synthesis. In W. R. Meehan, T. R. Merrell and T. A. Hanley (eds.). *Fish and wildlife relationships in old-growth forests: proceedings of a symposium.* Amer. Inst. of Fish. Res. Biol. Pp. 411-420.
- Dearden, B. L., R. E. Pegau, and R. M. Hansen. 1975. Precision of microhistological estimates of ruminant food habits. *J. Wildl. Manage.* 39:402-407.
- Fracker, S. B., and J. A. Brischle. 1944. Measuring the local distribution of *Ribes*. *Ecology* 25:283-303.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Ser., Gen. Tech. Rep. PNW-8.
- Gill, R. B., L. H. Carpenter, R. M. Bartmann, D. L. Baker, G. C. Schoonveld. 1983. Fecal analysis to estimate mule deer diets. *J. Wildl. Manage.* 47:902-915.
- Halpern, C. B., P. M. Frenzen, J. E. Means, and J. F. Franklin. 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *J. Veg. Sci.* 1:181-194.
- Hanley, T. A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. *J. Appl. Ecol.* 21:423-436.
- Hanley, T. A., F. L. Bunnell, E. E. Starkey, S. K. Stevenson, and A. S. Harestad. 1984. Habitat relationships of cervidae (deer) in old-growth forests. In *New forests for a changing world: Proc. 1983 Convention of Soc. Amer. Foresters*, Portland. Pp. 361-367.
- Hanley, T. A., R. G. Cates, B. Van Horne, and J. D. McKendrick. 1987. Forest stand-age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. In F. D. Provenza, J. T. Flinders, and E. D. McArthur (eds.). *Proc. Symp. Plant-Herbivore Interactions.* U.S.D.A. For. Serv., Gen. Tech. Rep. INT-222. Pp. 9-17.
- Hanley, T. A., and C. L. Rose. 1987. Influence of overstory on snow depth and density in hemlock-spruce stands: implications for management of deer habitat in southeast Alaska. U.S.D.A. For. Ser. Res. Note PNW-RN-459.
- Hanley, T. A., C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. *Ecology* 73:537-541.
- Happe, P. J., K. J. Jenkins, E. E. Starkey, and S. Sharrow. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. *J. Wildl. Manage.* 54:557-566.
- Harestad, A. S. 1979. Seasonal movements of black-tailed deer on northern Vancouver Island. Univ. British Columbia, Vancouver. Ph.D. Thesis.
- Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Methods for determining the nutritive quality of range ruminant diets: a review. *J. Anim. Sci.* 52:363-376.
- Isaac, L. A. 1940. Vegetative succession following logging in the Douglas-fir region with special reference to fire. *J. For.* 38:716-721.
- Janz, D. W. 1983. Seasonal composition and quality of Roosevelt elk diets on Vancouver Island. Univ. British Columbia, Vancouver. M. S. Thesis.
- Jenkins, K. J., and E. E. Starkey. 1980. Roosevelt elk of the Hoh Valley, Olympic National Park. Nat. Park Serv. Final Rep. 80-3. Oregon Cooperative Park Studies Unit, Oregon State Univ., Corvallis.
- _____. 1991. Food habits of Roosevelt elk. *Rangelands* 13:261-265.

- _____. 1993. Winter forages and diets of elk in old-growth and regenerating coniferous forests in western Washington. *Am. Midl. Nat.* 130:299-313.
- Leslie, D. M., Jr. 1983. Nutritional ecology of cervids in old-growth forests in Olympic National Park, Washington. Oregon State Univ. Corvallis. Ph.D. Thesis.
- Leslie, D. M., Jr., M. Vavra, E. E. Starkey, and R. C. Slater. 1983. Correcting for differential digestibility in micro-histological analyses involving common coastal forages of the Pacific Northwest. *J. Range Manage.* 36:730-732.
- Leslie, D. M., Jr., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. *J. Wildl. Manage.* 48:762-775.
- Leslie, D. M., Jr., E. E. Starkey, and B. G. Smith. 1987. Forage acquisition by sympatric cervids along an old-growth sere. *J. Mammal.* 68:430-434.
- Long, J. N., and J. Turner. 1975. Aboveground biomass of understorey and overstorey in an age sequence of four Douglas-fir stands. *J. Appl. Ecol.* 12:179-188.
- McArthur, C., A. Hagerman, and C. T. Robbins. 1991. Physiological strategies of mammalian herbivores against plant defenses. In R. T. Palo, and C. T. Robbins. (eds.) *Plant defenses against mammalian herbivory*. CRC Press, Boca Raton. Pp. 103-114.
- Means, J. E., McKee, W. E., Moir, W., and J. F. Franklin. 1982. Natural revegetation of the northeastern portion of the devastated area. In S.A.C. Keller (ed.). *Mount St. Helens: One year later*. Eastern Wash. Univ. Press. Pp. 222-230.
- Merrill, E. H. 1987. Population dynamics and habitat ecology of elk in the Mount St. Helens blast zone. Univ. Wash. Ph.D. Thesis.
- _____. 1994. Summer foraging ecology of wapiti in the Mount St. Helens blast zone. *Can. J. Zool.* 72:303-311.
- Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. *J. Wildl. Manage.* 45:323-334.
- Nyberg, J. B. and D. W. Janz. 1990. Deer and elk habitats in coast forests of southern British Columbia. Special Rep. Ser. No. 5, B.C. Ministry. For., Victoria. 310 pp.
- Paige, D. K. 1990. Elk use of meadow habitats in the Cedar River Drainage, Washington. Univ. of Wash., Seattle. Ph.D. Thesis.
- Raedeke, K. J., and J. F. Lemkuhl. 1985. A simulation procedure for modeling the relationships between wildlife and forest management. In J. Verner, M.L. Morrison and C. J. Ralph (eds.). *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Univ. of Wisconsin Press, Madison. Pp. 377-387.
- Raedeke, K. J., and R. D. Taber. 1982. Mechanisms of population regulation in western Washington forests for *Cervus* and *Odocoileus*. *Proc. Int. Congr. Game Biol.* 14:69-80.
- Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98-107.
- Robbins, C. T., S. Mole, T. A. Hanley, and A. E. Hagerman. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion. *Ecology* 68:1606-1615.
- Rochelle, J. A. 1980. Mature forests, litterfall and patterns of forage quality as factors in the nutrition of black-tailed deer on northern Vancouver Island. Univ. British Columbia, Vancouver. Ph.D. Thesis.
- Schoen, J. W., M. D. Kirchoff, and O. C. Wallmo. 1984. Sitka black-tailed deer/old-growth relationships in southeast Alaska: implications for management. In W. R. Meehan, T. R. Merrell and T.A. Hanley (eds.). *Fish and wildlife relationships in old-growth forests: proceedings of a symposium*. Amer. Instit. Fish. Res. Biol. Pp. 315-320.
- Schwartz, J. E., and G. E. Mitchell. 1945. The Roosevelt elk on the Olympic Peninsula. *J. Wildl. Manage.* 9:295-319.
- Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Company, New York.
- Smithey, D. A., M. J. Wisdom, and W. W. Hines. 1985. Roosevelt elk and black-tailed deer response to habitat changes related to old-growth forest conversion in southwest Oregon. In R. W. Nelson (ed.). *Proc. western states and provinces elk workshop*, Edmonton. Pp. 45-55.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and Company. San Francisco.
- Spalinger, D. E., Robbins, C. T., and Hanley, T. A. 1986. The assessment of handling time in ruminants: The effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. *Can. J. Zool.* 64:312-321.
- Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. *J. Range Manage.* 21:264-265.
- Stevens, R. G., J. K. Winjum, R. R. Gilchrist, and D. A. Leslie. 1987. Revegetation in the western portion of the Mount St. Helens blast zone during 1980 and 1981. In D. E. Bilderback (ed.) *Mount St. Helens 1980: botanical consequences of the explosive eruptions*. Univ. Calif. Press, Berkeley. Pp. 210-224.
- Stevenson, S. K., and J. A. Rochelle. 1984. Lichen litterfall—its availability and utilization. In W. R. Meehan, T. R. Merrell and T.A. Hanley (eds.). *Fish and wildlife relationships in old-growth forests: proceedings of a symposium*. Amer. Inst. Fish. Res. Biol. Pp. 391-396.
- Taylor, D. A. 1986. Roosevelt elk calf ratios from grassland versus forestland, N.W. Oregon. In D. Eastman (ed.) *Proc. Western States and Provinces Elk Workshop*, Oregon Dep. Fish and Wildl. Pp. 245-247.
- Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for *in vitro* digestion of forage crops. *J. Brit. Grassl. Soc.* 18:104-111.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. E. Fay, and B. L. Bradley. 1967. Protein requirements of white-tailed deer fawns. *J. Wildl. Manage.* 31:679-685.
- Vavra, M., and J. L. Holechek. 1980. Factors influencing micro-histological analysis of herbivore diets. *J. Range Manage.* 33:371-374.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. *Amer. Nat.* 108:290-304.
- Witmer, C. W., M. Wisdom, E. P. Harshman, R. J. Anderson, C. Carey, M. P. Kuttel, I. D. Luman, J. A. Rochelle, R. W. Scharpf, and D. Smithey. 1985. Deer and elk. In E. R. Brown (ed.) *Management of wildlife and fish habitats in forests of western Oregon and Washington*. U.S.D.A. For. Ser., R6-F&WL-192-1985. Pp. 231-258.
- Zahn, M. H. 1985. Use of thermal cover by elk (*Cervus elaphus*) on a western Washington summer range. Univ. Washington, Seattle. Ph.D. Thesis.

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Mark P. Zimmerman, Oregon Department of Fish and Wildlife, 17330 S.E. Evelyn Street, Clackamas, Oregon 97015
and

Robert M. Parker, 1617 College Drive, Apt. #2, Baton Rouge, Louisiana 70808

Relative Density and Distribution of Smallmouth Bass, Channel Catfish, and Walleye in the Lower Columbia and Snake Rivers

Abstract

We used two indices derived from catch and effort to compare density and relative abundance of smallmouth bass *Micropterus dolomieu*, channel catfish *Ictalurus punctatus*, and walleye *Stizostedion vitreum vitreum* among reaches (forebays, mid-reservoirs, tailraces) and reservoirs of the lower Columbia and Snake Rivers, and among unimpounded sampling zones in the Columbia River downstream from Bonneville Dam. Smallmouth bass density was highest in forebay and mid-reservoir reaches of Snake River reservoirs. Density was greatest in lower Snake River reservoirs, intermediate in Columbia River reservoirs, and lowest in the Columbia River downstream from Bonneville Dam. Smallmouth bass were most abundant in Lower Granite Reservoir. Channel catfish were distributed throughout all reaches within reservoirs. Density was far greater in the Snake River than in the Columbia River. Walleye density was low throughout the lower Columbia River, and walleye were absent in the Snake River upstream from Ice Harbor Dam. Distribution and relative abundance of introduced piscivorous fishes indicate that predator-prey relationships differ among reservoirs, between impounded and unimpounded reaches, and between the lower Snake and Columbia rivers. Differences in the relative abundance of introduced predators should contribute to variation in losses of juvenile salmonids to resident predators.

Introduction

Fish communities in the Columbia River basin have been shaped by a combination of numerous species introductions and extensive habitat alterations following impoundment. Slower water velocities and warmer temperatures in impoundments have increased the habitat available to populations of exotic warm and cool water species, most notably smallmouth bass *Micropterus dolomieu*, channel catfish *Ictalurus punctatus*, and walleye *Stizostedion vitreum vitreum* (Poe *et al.* 1991). Their growing populations are supporting new sport fisheries of increasing recreational and economic importance, particularly in light of the dwindling stocks of Columbia River salmon *Oncorhynchus* spp. and steelhead *O. mykiss*. Region-wide interest in smallmouth bass, channel catfish, and walleye stems not only from their potential to enhance sport fishing opportunities, but from justifiable concern regarding the impacts of introduced predators on fishes native to the Columbia and Snake Rivers.

The annual downstream migration of juvenile anadromous salmonids through the Columbia and Snake Rivers represents a potential seasonal food resource for piscivorous fishes. Impoundments prolong migration rates of juvenile salmon and steelhead, concentrate them at dams, and increase their susceptibility to predation (Ebel 1977, Raymond 1979, 1988). The magnitude of predation losses

relative to other sources of mortality can be significant (Rieman *et al.* 1991). Although northern squawfish *Ptychocheilus oregonensis* accounted for most of the predation-related mortality in John Day Reservoir from 1983 to 1986 (Rieman *et al.* 1991), smallmouth bass, channel catfish, and walleye also consumed juvenile salmonids (Vigg *et al.* 1991). Introduced predators undoubtedly interact with and prey on resident native species including northern squawfish, although the impact of these interactions has not been extensively studied.

Determining predator distributions in the lower Columbia River basin is a first step towards increasing our understanding of the impacts of introduced predators. Unfortunately, most of the pertinent information on Columbia River basin fish communities resides in institutional documents of limited circulation, with the exception of Beamesderfer and Rieman (1991). Additionally, logistical problems associated with sampling large river systems have limited the geographical scope of individual research efforts in the Columbia River basin. We gathered standardized catch and effort data for smallmouth bass, channel catfish, and walleye throughout the lower Columbia and Snake Rivers from 1990 to 1992. In this paper, we compare density and relative abundance of each species among reservoirs in the lower Snake and Columbia Rivers, and in the unimpounded Columbia River downstream from Bonneville Dam. We also

examine distributional differences among reaches (forebay, mid-reservoir, and tailrace) within reservoirs.

Methods

Field Sampling

We sampled from 1990 through 1992 to collect information on resident piscivorous fishes throughout the lower Columbia and lower Snake Rivers. Because the large size of the area precluded our sampling all reservoirs in the same year, we sam-

pled fish in Columbia River reservoirs (Bonneville, The Dalles, John Day, and McNary) in 1990, Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, and Lower Granite) in 1991, and the Columbia River downstream from Bonneville Dam in 1992 (Figure 1). We sampled John Day Reservoir in 1990, 1991 and 1992 in order to examine annual variability.

We usually sampled three, 6-kilometer long reaches in each reservoir: forebay (immediately upstream from the dam), mid-reservoir, and tailrace (immediately downstream from the next dam). Two

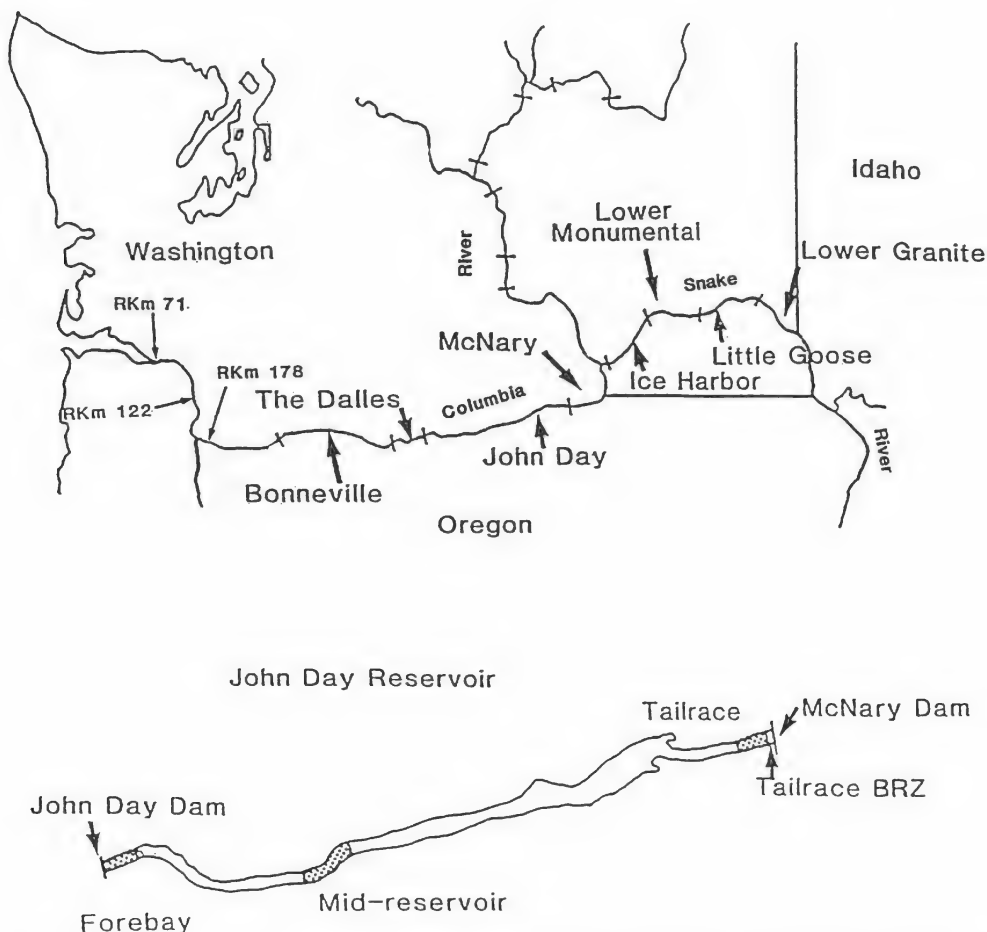


Figure 1. Sampling areas in the lower Columbia River basin. Small arrows indicate boundaries between sampling zones downstream from Bonneville Dam sampled in 1992. Large arrows indicate Columbia River reservoirs sampled in 1990, and Snake River reservoirs sampled in 1991. Map of John Day Reservoir illustrates reaches sampled within reservoirs.

exceptions were (1) the upper reach of Lower Granite reservoir was not in the tailrace of a dam, and (2) we sampled four reaches in McNary Reservoir: forebay, mid-reservoir, tailrace of Ice Harbor Dam, and the upper reservoir immediately upstream from the confluence of the Columbia and Snake Rivers. Because of its size, we partitioned the Columbia River downstream from Bonneville Dam into three zones: River kilometer (Rkm) 71-121, Rkm 122-177, and Rkm 178-234. The upper zone included Bonneville Dam tailrace. Sampling in each zone was stratified by lower, middle, and upper reaches (analogous to forebay, mid-reservoir, and tailrace reaches within reservoirs). All reaches were subdivided into 24 nearshore sampling sites of equal length.

We sampled fish with three gears: an electrofishing boat, bottom gill nets, and surface gill nets. We electrofished parallel to shore, with current of approximately 4 amperes. Bottom and surface gill nets were fished perpendicular to shore, and measured 46-m long by 2.4-m deep, with alternating panels of 3.2, 4.4, and 5.1-cm bar mesh. Sites within each reach were sampled from 0300 to 1200 hours in the order in which they were randomly selected on a daily basis from the numbers set of 1-24. We completed a minimum of 24, 15-minute power-on electrofishing runs, 24, 1-h bottom gill-net sets, and 24, 1-h surface gill-net sets in each reach. Total effort in each reach is

summarized in Table 1. Smallmouth bass, channel catfish, and walleye were counted and measured (fork length in mm).

Gear Selectivity

We compared mean catch per unit of effort (CPUE) for fish of all fork lengths to evaluate selectivity among gears for each species. We selected the most effective gear to calculate density indices for each species based on CPUE.

Density

We used CPUE as an index of density of each species in each sampling area. We also calculated a second index of density derived from frequency distributions of CPUE. Although CPUE is a commonly used index of fish density (or abundance when population size is known), Bannerot and Austin (1983) recommended the use of the square root of the relative frequency of zero-fish catches. The zero-catch index is inversely related to density such that low values correspond to high fish densities. Therefore, we used the reciprocal (1/square root of the proportion of zero catches) so the index would be directly proportional to density. This adjustment created a problem in the mid-reservoir of Lower Granite Reservoir, where at least one smallmouth bass was captured in every electrofishing run, and the proportion of zero catches equaled

TABLE 1. Total effort (spring and summer) by sampling gear and reach in zones downstream from Bonneville Dam (1992), Columbia River reservoirs (1990), and Snake River reservoirs (1991). Units of effort are number of 15" electrofishing runs, and 1-h bottom and surface gill-net sets. Reaches are FB (forebay), MR (mid-reservoir), TR (tailrace), and UR (upper reservoir).

Reservoir or zone	Effort by Sampling Gear and Reach											
	Electrofishing				Bottom gillnet				Surface gillnet			
	FB	MR	TR	UR	FB	MR	TR	UR	FB	MR	TR	UR
Rkm 71-121	—	130	—	—	—	157	—	—	—	158	—	—
Rkm 122-177	—	128	—	—	—	79	—	—	—	81	—	—
Rkm 178-234	—	126	37	—	—	70	31	—	—	67	32	—
Bonneville	23	27	27	—	26	21	24	—	16	23	29	—
The Dalles	38	12	30	—	26	23	24	—	27	21	24	—
John Day	35	37	31	—	18	30	30	—	26	34	29	—
McNary	34	37	31	30	30	28	27	32	28	27	25	34
Ice Harbor	33	33	43	—	43	37	37	—	43	38	37	—
Lower Monumental	42	37	33	—	40	43	41	—	40	40	43	—
Little Goose	37	31	33	—	40	36	38	—	40	37	38	—
Lower Granite	35	34	—	33	43	44	—	50	42	47	—	46

TABLE 2. Surface areas (hectares) of zones downstream from Bonneville Dam and reaches within Columbia and Snake River reservoirs. Near-shore areas are the total mid-reservoir areas minus those areas greater than 12.2 m deep and greater than 46 m from shore.

Reservoir or reach	Surface area (hectares)					
	Total	Forebay	Mid-reservoir		Tailrace	Upper
			Total	Near-shore		
RKm 71-121	7,604	—	—	6,421	—	—
RKm 122-177	6,072	—	—	5,080	—	—
RKm 178-234	6,123	—	5,715	5,119	408	—
Bonneville	7,632	390	6,866	2,919	376	—
The Dalles	3,639	526	2,631	1,604	479	—
John Day	19,781	792	18,171	7,933	810	—
McNary	12,218	863	10,508	5,579	206	641
Ice Harbor	3,285	578	2,420	1,452	287	—
Lower Monumental	2,425	421	1,639	620	365	—
Little Goose	3,888	599	3,086	1,492	203	—
Lower Granite	3,240	594	2,306	1,236	—	340

zero. We therefore assigned a zero-fish catch index value to that reach based on the proportional difference in CPUE between the mid-reservoir reaches in Little Goose and Lower Granite reservoirs.

We pooled data from lower, middle, and upper reaches to compare mean CPUE and zero-catch indices among the three zones of the Columbia River downstream of Bonneville Dam. We pooled data from Columbia River reservoirs and Snake River reservoirs to compare mean CPUE and zero-catch indices among forebay, mid-reservoir, and tailrace reaches within each river. We described 95% confidence intervals for CPUE indices as plus and minus two standard errors of mean CPUE.

We calculated reservoir-wide CPUE and zero-catch indices by taking the product of each reach-specific index and the proportion of total reservoir surface in that reach (Table 2), and summing the products across reaches. Each reservoir-wide density index was therefore a weighted mean, where the relative surface area of the forebay, mid-reservoir, and tailrace was used as a weighting factor for the corresponding reach-specific index values. Standard errors for reservoir-wide CPUE indices were estimated using a BASIC program that generated a random, normal distribution of 500 reservoir-wide CPUE indices based on the mean and standard error of CPUE in each reach (forebay, mid-reservoir, and tailrace) within each reservoir. We described 95% confidence intervals as

plus and minus two standard errors. Our approach was similar to Rieman *et al.* (1991), who used a Monte Carlo simulation to estimate standard deviation of the number of salmonids consumed by predators.

Our sampling sites were limited to nearshore areas throughout the lower Columbia and Snake Rivers. Therefore, we estimated the surface area in mid-reservoirs and the three zones downstream from Bonneville Dam that was both less than 12.2 m and within 46 m of shore (Table 2). We used these near-shore surface areas as the weighting factor for the corresponding reach-specific density indices when calculating reservoir-wide indices for each species.

Relative Abundance

We calculated an index of relative abundance as the product of each reservoir-wide CPUE density index (or zone-specific CPUE downstream from Bonneville Dam) and corresponding reservoir surface area (Table 2). We expressed relative abundance in each reservoir and zone as a proportion of the reservoir or zone with the highest observed index value.

Results

Smallmouth Bass

Electroshocking accounted for approximately 91% of the total catch of 7,227 smallmouth bass.

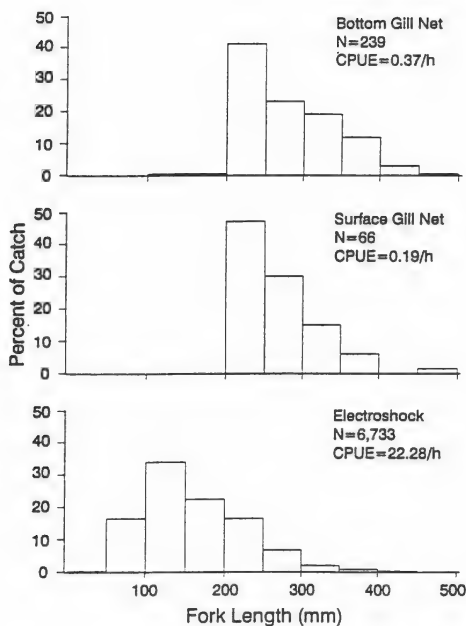


Figure 2. Size composition and catch per unit effort (CPUE) of smallmouth bass by gear type. N=number of fish measured.

Electroshocking CPUE was 60 times greater than bottom gill-net CPUE, and 117 times greater than surface gill-net CPUE (Figure 2). Fish from 100 to 149 mm fork length represented the largest proportion of the electrofishing catch, whereas nearly all fish captured in gill nets were greater than 200 mm. We used electrofishing catch and effort data to calculate density indices.

Density of smallmouth bass downstream from Bonneville Dam was highest in the two up-river zones and lowest from Rkm 71-121 (Figure 3). Density was similar among forebay, mid-reservoir, and tailrace reaches of Columbia River impoundments, but was higher in forebay and mid-reservoirs than tailraces of Snake river impoundments. The CPUE and zero-catch indices yielded similar differences in density among reaches and zones. Density was greatest in Snake River reservoirs, intermediate in Columbia River reservoirs, and lowest downstream from Bonneville Dam for both indices (Figure 4). Relative abundance of smallmouth bass was greatest in Lower Granite Reservoir and lowest in the unimpounded Columbia River

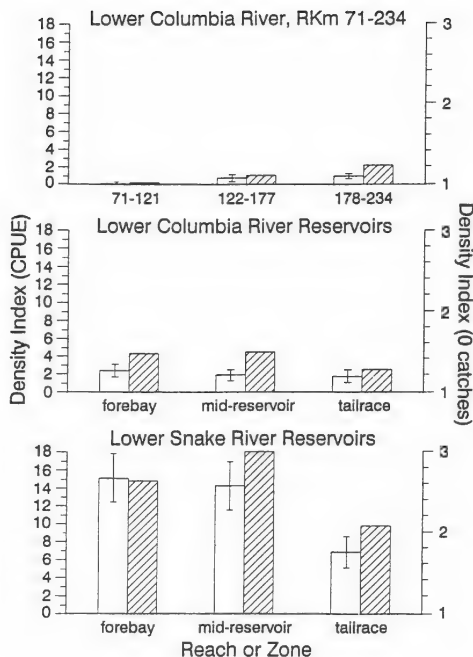


Figure 3. Indices of smallmouth bass density in sampling zones of the lower Columbia River downstream from Bonneville Dam, in reaches of Columbia River reservoirs (Bonneville, The Dalles, John Day, McNary), and in reaches of Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, Lower Granite). Indices are electrofishing CPUE (open bars) and the relative frequency of zero catches for electrofishing (hatched bars). Error bars indicate 95% confidence intervals around mean CPUE.

from Rkm 71 to 121. Relative abundance in Snake River reservoirs was high, considering their small size relative to Columbia River reservoirs.

Electrofishing catch rates of smallmouth bass in John Day Reservoir were very similar from 1990 through 1992. Reservoir-wide density indices were 3.01 in 1990, 3.46 in 1991, and 4.47 in 1992. Density in the tailrace was less than in the forebay and mid-reservoir each year. In any year, density of smallmouth bass in John Day Reservoir was less than in Snake River reservoirs sampled in 1991, and an order of magnitude greater than Columbia River zones downstream from Bonneville Dam sampled in 1992.

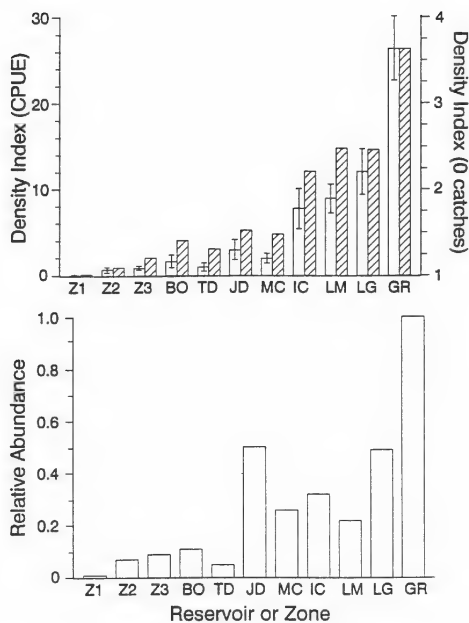


Figure 4. Indices of smallmouth bass density and relative abundance in sampling zones in the Columbia River downstream from Bonneville Dam, and in Columbia and Snake River reservoirs. Error bars indicate 95% confidence intervals around mean CPUE. Density indices are as described for Figure 3. Relative abundance is the product of reservoir-wide CPUE density indices and the corresponding surface areas. Lower Columbia River sampling zones are RKM 71-121 (Z1), RKM 122-177 (Z2), and RKM 178-234 (Z3). Reservoirs are Bonneville (BO), The Dalles (TD), John Day (JD), McNary (MC), Ice Harbor (IH), Lower Monumental (LM), Little Goose (LG), and Lower Granite (GR).

Channel catfish

We sampled 2,392 channel catfish with all gears. Bottom gill nets accounted for 78% of the total catch (Figure 5). Bottom gill nets selectively sampled fish greater than 200 mm fork length. Electroshocking was more effective at sampling both very small (<100 mm) and very large (>600 mm) fish when compared to bottom gill nets; however, very few small and large fish were captured by electrofishing because overall CPUE was one sixth that of bottom gill nets. We used catch and effort data from bottom gill-net sampling to calculate indices of channel catfish density.

No channel catfish were captured downstream from Bonneville Dam. Both CPUE and zero-catch

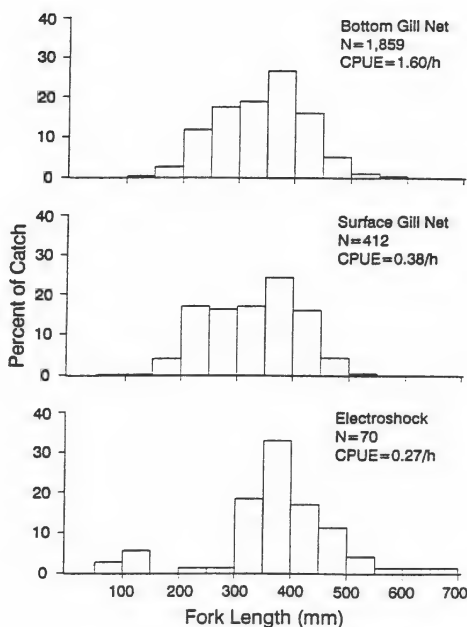


Figure 5. Size composition and catch per unit effort (CPUE) of channel catfish by gear type. N = number of fish measured.

indices for channel catfish were highest in tailraces of Columbia River reservoirs (Figure 6). Catch per unit effort among reaches within Snake River reservoirs was higher in mid-reservoirs and tailraces than forebays, whereas the zero-catch index was lower in forebays and mid-reservoirs than tailraces (Figure 6). We captured channel catfish in each Columbia River reservoir; however, catches were extremely low except in McNary Reservoir. We therefore restricted our reservoir-wide comparisons of density and relative abundance to McNary Reservoir and the four Snake River reservoirs. Density of channel catfish was highest in Ice Harbor Reservoir and lowest in McNary and Lower Granite reservoirs (Figure 7). Differences in reservoir-wide density were similar between the CPUE and zero-catch indices. Relative abundance was more than twice as great in Ice Harbor Reservoir than in any of the other reservoirs (Figure 7).

Bottom gill-net catch rates of channel catfish in John Day Reservoir were variable from 1990 through 1992, primarily because catches in all three years were very low. Only 4 were sampled in 1990, 16 in 1991, and 15 in 1992. Catch rates

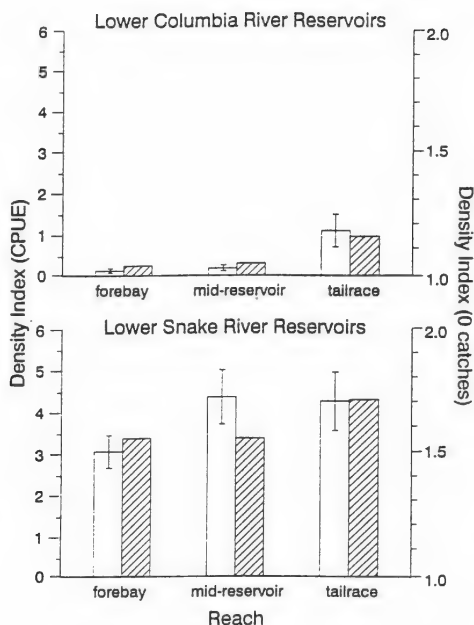


Figure 6. Indices of channel catfish density in reaches of Columbia River reservoirs (Bonneville, The Dalles, John Day, McNary) and Snake River reservoirs (Ice Harbor, Lower Monumental, Little Goose, Lower Granite). Indices are bottom gill-net CPUE (open bars) and the relative frequency of zero catches for bottom gill nets (hatched bars). Error bars indicate 95% confidence intervals around mean CPUE.

were greatest in the tailrace reach of John Day Reservoir in each year. In any year, density of channel catfish in John Day Reservoir was at least an order of magnitude less than density in Snake River reservoirs sampled in 1991.

Walleye

Only 88 walleye were captured during the study. Catch per hour was 0.16 for electroshocking, 0.03 for bottom gill nets, and <0.01 for surface gill nets. Walleye captured by electroshocking ranged from 150 to 750 mm fork length, whereas those captured in bottom gill nets ranged from 350 to 600 mm. Only 3 walleye were captured in surface gill nets.

Because of the small sample size for all gears, we did not calculate density indices for walleye. We can offer the following observations on walleye distribution. We captured walleye throughout

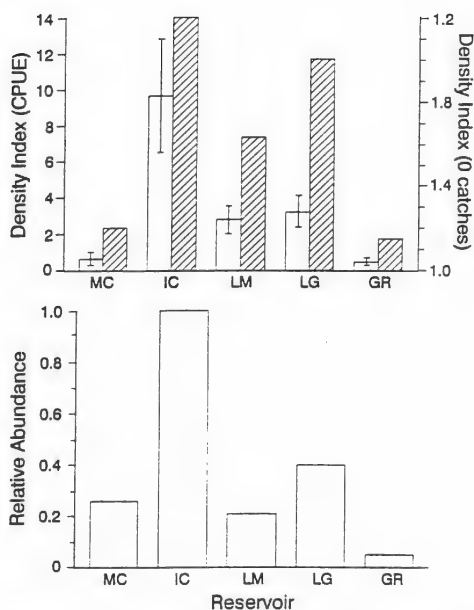


Figure 7. Indices of channel catfish density and relative abundance in McNary (MC), Ice Harbor (IC), Lower Monumental (LM), Little Goose (LG), and Lower Granite (GR) reservoirs. Error bars indicate 95% confidence intervals around mean CPUE. Density indices are as described for Figure 6. Relative abundance is the product of reservoir-wide CPUE density indices and the corresponding surface areas.

much of the lower Columbia River, from Rkm 137 to upper McNary Reservoir, and in the Snake River from the mouth to Ice Harbor Dam tailrace. No walleye were captured in the Snake River reservoirs. Catch rates were highest in tailraces, intermediate in mid-reservoirs, and very low in forebays. Downstream from Bonneville Dam, catch rates were highest from Rkm 178 to 234. Among Columbia River reservoirs, catch rates were highest in The Dalles Reservoir, followed in order by Bonneville, John Day, and McNary reservoirs.

Discussion

Differences in the density and relative abundance of introduced predators within and among reservoirs were striking, particularly when compared with density and relative abundance of northern squawfish (Ward *et al.* in press). Density of smallmouth bass was generally greatest in forebays and mid-reservoirs, whereas density of northern squawfish was greatest in tailraces. Smallmouth bass densities were greatest upstream from John

Day Dam, particularly in the Snake River, whereas northern squawfish density is greatest in the lower Columbia River downstream from John Day Dam. Density of channel catfish was highest in Snake River reservoirs, particularly in tailrace restricted zones. Walleye distribution was limited to the Columbia River and the Snake River downstream from Ice Harbor Dam. Our catch rates of walleye in reservoirs were low but consistent with recent sport angling success (Tinus and Beamesderfer 1994). Recreational fishery surveys conducted in lower Columbia River reservoirs showed CPUE was greatest in The Dalles Reservoir, followed in order by Bonneville and John Day reservoirs (Tinus and Beamesderfer 1994).

In general, impoundments contained higher densities of introduced predators than the unimpounded Columbia River downstream from Bonneville Dam. Ward *et al.* (in press) reported that density and abundance of northern squawfish was relatively high in the unimpounded Columbia River. The high density of northern squawfish downstream from Bonneville Dam is noteworthy because some authors have suggested that impoundments have enhanced northern squawfish populations (Poe *et al.* 1991). Northern squawfish occurred in the diets of smallmouth bass and walleye in John Day Reservoir (Poe *et al.* 1991). Other native species commonly eaten by introduced predators include cottids and catostomids. Our results indicate that predation by introduced species on juvenile northern squawfish and other native species may be greater in reservoirs than unimpounded reaches.

Many differences exist between lower Columbia River and lower Snake River reservoirs that might contribute to higher densities of smallmouth bass and channel catfish in the Snake River. Water temperatures during summer are higher in the lower Snake River than in the lower Columbia River, sometimes creating a thermal barrier to adult salmonids returning to the Snake River (Trefethen 1972). Snake River reservoirs are generally smaller, have greater mean depths, and are more isolated and less accessible to anglers than Columbia River reservoirs. The effect of these factors, and undoubtedly many other habitat features, on the proliferation of smallmouth bass and channel catfish has not been studied. In the course of our sampling, we observed that densities of other introduced warm water species such as white crappie *Pomoxis annularis*, black crappie *P.*

nigromaculatus, and pumpkinseed *Lepomis gibbosus* are also much greater in the lower Snake River than the lower Columbia River.

Our findings suggest that the magnitude and dynamics of predation by resident fishes on juvenile salmonids are quite different in the lower Snake River than the lower Columbia River. Losses of juvenile salmonids to predation by northern squawfish are greater in the lower Columbia River than the lower Snake River (Ward *et al.* in press). Our study has shown that relative abundance of smallmouth bass and channel catfish was much greater in the Snake River than the Columbia River. Diet and consumption rates of channel catfish in John Day Reservoir (Poe *et al.* 1991, Vigg *et al.* 1991) indicated that they may be important predators on juvenile salmonids, particularly in tail-races. Daily consumption rates of juvenile salmonids by smallmouth bass exceeded those by northern squawfish in the Columbia River near Richland, Washington (Tabor *et al.* 1993).

Introduced predators might be expected to consume greater numbers of juvenile salmonids in the Snake River than in the Columbia River; however, several factors may limit predation by smallmouth bass and channel catfish. Peak migration of juvenile salmonids past Snake River dams occurs in spring, when cool water temperatures would lower consumption rates of predators. Many juvenile salmonids are collected at Lower Granite and Little Goose dams and transported to the Columbia River downstream from Bonneville Dam, reducing their availability to resident predators in impoundments, particularly in Ice Harbor and Lower Monumental reservoirs.

Populations of all predator species could be affected by a predator control program begun in 1990 to reduce northern squawfish predation on juvenile salmonids. If mortality of juvenile salmonids is significantly reduced by sustained harvest of northern squawfish, predation by other species may be enhanced due to increased availability of juvenile salmonid prey. A change in growth rate might accompany dietary shifts, altering size distributions, fecundity, or abundance, as was shown for yellow perch *Perca flavescens* following removal of white suckers *Catostomus commersoni* (Hayes *et al.* 1992). Conversely, both smallmouth bass and walleye are harvested incidentally by anglers fishing for northern squawfish. Angling for walleye has increased throughout the lower Columbia River (Tinus and Beamesderfer 1994), but exploitation

rates have not been determined. Additional harvest of smallmouth bass and walleye could be significant, particularly in areas where abundance appears low.

Several uncertainties limited our comparison of relative density and abundance among reservoirs. We excluded deep (>12.2 m), mid-channel (>46 m from shore) areas when calculating reservoir-wide indices of density and abundance because our sampling was limited to near-shore areas. If smallmouth bass or channel catfish utilize mid-channel areas to a significant extent, we would have underestimated their density and abundance, particularly in large reservoirs where mid-reservoir reaches are proportionally large.

We recognize that comparing Columbia River reservoirs, Snake River reservoirs, and the unimpounded lower Columbia River may be uncertain because sampling in each area was conducted in different years. This uncertainty was at least partly ameliorated by sampling John Day Reservoir each year. The rank order of the density index for smallmouth bass in John Day Reservoir among the 11 sampling areas (8 reservoirs and 3 unimpounded zones) was the same in any year.

Any index of fish density or abundance has shortcomings. The relationship of CPUE to abundance is not always one of strict proportionality (Richards and Schnute 1986). Bannerot and Austin (1983) evaluated statistical bias in CPUE relative to several other indices that are based on frequency distributions of catch. They showed the square root of the relative frequency of zero catches to be an unbiased index of density, and recommended its use over CPUE. Our results based on the zero-catch index were generally similar to those based on CPUE.

Although both indices yielded similar results, the index based on the proportion of zero catches had several limitations. It is inversely related to

density such that low index values corresponded to high fish densities, although this was easily overcome by using the reciprocal. This adjustment created a problem when the proportion of zero catches equaled zero, suggesting that the utility of the index may be limited to areas with low to moderate densities of fish. Additionally, frequency distributions of catch and effort yield a single index value without variance. Nevertheless, we believe the validity of our findings was reinforced by the fact that both indices yielded similar patterns of density differences among areas and reservoirs, although we acknowledge that indices are practical surrogates for more robust approaches to population estimation, such as mark-recapture methodologies.

Our results present a picture of the current distribution and relative abundance of introduced piscivorous fishes in the lower Columbia River basin. Despite uncertainties, we believe that predator distributions provide strong evidence that important differences exist in predator-prey relations among reservoirs, between impounded and unimpounded reaches, and between the lower Columbia and Snake rivers.

Acknowledgements

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Literature Cited

- Bannerot, S. P., and C. B. Austin. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. *Transactions of the American Fisheries Society* 112:608-617.
- Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:439-447.

- Ebel, W. J. 1977. Panel 2: Fish passage problems and solutions—major passage problems. In E. Schwiebert (ed.), *Columbia River Salmon and Steelhead*. American Fisheries Society, Special Publication No. 10, Washington, D.C. Pp. 33-39.
- Hayes, D. B., W. W. Taylor, and J. C. Schneider. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. *Transactions of the American Fisheries Society* 121:36-53.

- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Predergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405-420.
- Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* 108:505-529.
- Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. *North American Journal of Fisheries Management* 8:1-24.
- Richards, L. J., and J. T. Schnute. 1986. An experimental and statistical approach to the question: Is CPUE an index of abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 43:1214-1227.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:448-458.
- Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management* 13:831-838.
- Tinus, E. S., and R. C. Beamesderfer. 1994. An update on the distribution, fisheries, and biology of walleye in the lower Columbia River. Information Report Number 94-3, Oregon Department of Fish and Wildlife, Portland.
- Trefethen, P. 1972. Man's impact on the Columbia River. In R. T. Oglesby (ed.), *River Ecology and Man*. Academic Press, New York. Pp. 77-98.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421-438.
- Ward, D. L., J. H. Peterson, and J. Loch. In Press. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and the lower Snake River. *Transactions of the American Fisheries Society*.

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Intertidal Diatoms from Willapa Bay, Washington: Application to Studies of Small-Scale Sea-Level Changes

Abstract

Sea-level reconstructions using estuarine diatoms are generally constrained by the absence of detailed ecological data regarding the distributions of modern intertidal species. As part of an on-going study to assess the biostratigraphic record of relative sea-level changes triggered by earthquakes in the Pacific Northwest, modern intertidal diatoms were collected in surface samples from northern Willapa Bay, Washington. Q-mode factor analysis was used to classify assemblages from tidal flats and banks, shallow subtidal channels, low and high marshes along two intertidal transects on the Niihau River, and in intertidal samples from the open bay. Autochthonous taxa dominated the assemblages, but in some cases probable allochthonous taxa scored relatively high in the factor analysis.

The results of the analysis suggests that diatoms can be used to identify three elevational zones relative to tidal level: (1) intertidal flats, channel banks, and shallow subtidal channels, below approximate mean lower high water (MLHW); (2) low marshes approximately between MLHW and mean higher high water (MHHW); and (3) high marshes approximately between MHHW and extreme high water (EHW). The marsh-upland transition, near EHW, coincides with the terminus of regular diatom productivity and is recognizable by the disappearance of high-marsh diatoms in soil deposits. Absolute elevations of the ecological zones are constrained by local tidal range. Because of the cosmopolitan distributions of many of the species observed in this study, these data are probably applicable to studies of Quaternary sea-level change and paleoseismicity throughout the coastal Pacific Northwest.

Introduction

The purpose of this study is to identify diatom taxa associated with vertically distributed estuarine deposits (i.e., high marshes, low marshes, tidal flats, sloughs, and banks) that can be used to reconstruct small-scale (< 3 m) paleo-sea-level changes related to paleoseismicity or eustatic processes in the Pacific Northwest. Transitions between marine and freshwater diatoms in coastal deposits are commonly used to identify major transgressions and regressions of Quaternary sea level (e.g., Palmer and Abbott, 1986; Eronen *et al.*, 1987), but the recognition of small-scale changes in paleo-sea-level must be based on more subtle changes in vertically distributed assemblages. Such studies are invariably hindered by the paucity of detailed data regarding the modern distributions of pertinent taxa (e.g., Eronen *et al.*, 1987).

Compelling stratigraphic evidence now suggests that some changes in relative sea-level in the Pacific Northwest during the Holocene may have resulted from large earthquakes, including a moment magnitude (M_w) > 8 event as recently as about 300 years ago (Atwater, 1987, 1992; Darienzo and Peterson, 1990; Atwater and Yamaguchi, 1991; Atwater *et al.*, 1991; Nelson, 1992; Clarke and Carver, 1992; Nelson and Personius, in press; Clague and Bobrowsky, 1994). Some of the paleo-earthquakes have been attributed to rupture

along the Cascadia subduction zone, the boundary between the Juan de Fuca plate and the overriding North America plate (Figure 1), whereas others are believed to have been caused by displacements on shallow crustal faults (Nelson, 1992; Bucknam *et al.*, 1992; Nelson and Personius, in press). Coseismic land-level changes may result in sudden subsidence (e.g., Plafker, 1969; Atwater, 1987, 1992; Darienzo and Peterson, 1990; Nelson, 1992; Clarke and Carver, 1992) or uplift (Plafker, 1969; Bucknam *et al.*, 1992) of coastal and estuarine sites. The ecological consequences involve either a rapid rise or fall in relative sea level such that vegetated areas normally above the reach of tides are suddenly inundated, or conversely, normally intertidal surfaces are elevated out of the intertidal zone. Estimates of coseismic subsidence caused by the earthquake about 300 years ago range from about 0.5 m (Clarke and Carver, 1992; Darienzo and Peterson, 1990) to 2 m (Atwater, 1987; Atwater and Yamaguchi, 1991). This range in elevational change would be enough to quickly transform a lowland coastal meadow or forest into a tidal flat. Based on stratigraphic and biostratigraphic evidence in southwestern Washington, this process may have been repeated at least six times in about the last 3500 years (Atwater, 1988; Hemphill-Haley, unpub. data).

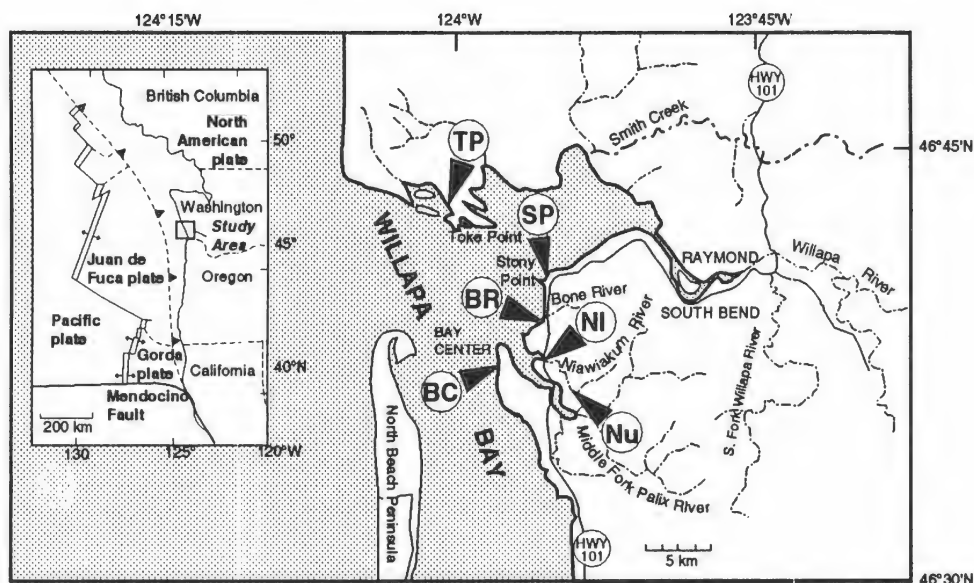


Figure 1. Willapa Bay, a mesotidal estuary in southwestern Washington. Sampling localities: BC—Bay Center tidal flat; BR—Bone River tidal flat; NI—transect NI, lower Niawia River; SP—Stony Point; Nu—transect Nu, upper Niawia River; TP—Toke Point.

Various kinds of coastal environments can be identified based on the classification of diatoms into ecological groups (Vos and de Wolf, 1988; 1993; Kosugi, 1988). In this paper, Q-mode factor analysis is used to cluster samples with similar diatom assemblages from the modern surfaces of tidal flats, intertidal river banks, shallow subtidal channels, low marshes, and high marshes in northern Willapa Bay, Washington (Figure 1). Upland samples, found to be barren of *in situ* diatoms, were excluded from the factor analysis.

Studies of modern estuarine diatoms have shown that many taxa are cosmopolitan (i.e., have a worldwide distribution) (McIntire and Moore, 1977; Tynni, 1986) and usually exhibit broader tolerances for salinity (Moore and McIntire, 1977; McIntire, 1978; Amspoker and McIntire, 1978; Admiraal, 1979) than for other factors such as exposure (Castenholz, 1963; Sullivan, 1978) and substrate (Amspoker and McIntire, 1978; Whiting, 1983; Whiting and McIntire, 1985; Kosugi, 1987). A series of ecological studies in Oregon documented the modern vertical distributions of attached or sediment-associated species in the lower part of the intertidal zone (Castenholz, 1963;

Riznyk and Phinney, 1972; Riznyk, 1973; Main and McIntire, 1974; Moore and McIntire, 1977; Amspoker and McIntire, 1978), but other than Nelson and Kashima (1993), differences in assemblages between tidal flats, marshes, and uplands have not been documented, and there are no such previous studies for coastal southwestern Washington.

Background

General Ecological Zonation Relative to Tidal Level

The mixed tides of the Pacific coast along southwestern Washington cause a fairly predictable three-tiered intertidal zonation, with lower intertidal flats, "low" marshes, and "high" marshes (Macdonald, 1977a; Macdonald and Barbour, 1977; Frey and Basan, 1985). The elevational ranges of these zones depends on the local tidal range, which varies both along the coast in the Pacific Northwest and within individual estuaries. In Willapa Bay, the tidal range between mean high water (MHW) and mean low water (MLW) ranges from 2.3 m near the mouth of the estuary to 3.4 m at its southernmost reaches (Major, 1989).

The initiation of low marsh vegetation in the Pacific Northwest is approximately equivalent to the elevation of mean lower high water (MLHW) (Macdonald and Barbour, 1977) and extends to approximately mean higher high water (MHHW), although vegetation is generally thicker between mean high water (MHW) and MHHW. Low marshes are commonly submerged once each tidal day (Frey and Basan, 1985) and thus support macrophytes capable of regular submergence. Sayce (1988) listed the dominant low-marsh macrophytes in Willapa Bay as *Salicornia virginica*, *Jaumea carnosa*, *Triglochin maritima*, and *Plantago maritima*. High marshes extend from MHHW to near extreme high water (EHW) (Macdonald and Barbour, 1977) and are submerged only during highest spring tides and storm surges. According to Frey and Basan (1985), high marshes are prone to desiccation because they "may remain continuously exposed for periods exceeding 10 days, between tidal inundations." Typical high-marsh macrophytes of Willapa Bay include *Distichlis spicata*, *Deschampsia caespitosa*, and *Agrostis alba*, with *Juncus balticus* and *Potentilla pacifica* at the highest levels (Sayce, 1988).

Tidal flats of the open estuary and channel banks of tidal rivers feeding the estuary extend downward from MLHW to approximately mean lower low water (MLLW). These flats and banks comprise a broad, mostly unvegetated region populated primarily by sediment-associated diatoms (Riznyk, 1973; Rao and Lewin, 1976; Amspoker and McIntire, 1978). *Zostera* spp. (eelgrass) beds may be present to provide a substrate for epiphytic diatoms, with *Z. marina* commonly found near MLLW and *Z. nana* found in the upper part of the zone, closer to MLHW. Shallow subtidal channels, as used in this study, refer to the river-channel floor less than 4 m below MLLW, which were sampled to determine whether this zone could be differentiated from the lower intertidal zone. As shown below, diatoms consist dominantly of allochthonous valves from the lower intertidal zone.

Methods

Sample collection

Results are based on diatom counts for 89 surface samples collected in 1990 in northern Willapa Bay (Figure 1). Samples BC-1, BC-2, and BC-3, from the Bay Center sand flat, were collected approxi-

mately 800, 500, and 200 m from shore, respectively. The flat is vegetated with sparse *Zostera nana* at the locations of samples BC-2 and BC-3. Samples BR-1 and BR-2 were collected from the unvegetated surface of a silty tidal flat north of the Bone River, approximately 150 and 300 m from shore. Samples were collected from the marsh and adjacent tidal flat at Stony Point: SP-1 and SP-2 are from the unvegetated flat; SP-3 is from the flat adjacent to a patch of *Triglochin maritima*; SP-4 is from a low marsh thickly vegetated with *Triglochin maritima* and *Salicornia virginica*; and SP-5 is from a high marsh in a thick stand of *Potentilla pacifica*, 3 m from the base of a Pleistocene terrace. Samples were collected from a marsh and tidal slough at Toke Point: TP-1 is from the floor of a sandy tidal slough covered with *Zostera marina* beds; TP-2 from a 1-m-diameter patch of *Triglochin maritima* at the marsh-to-flat transition; and TP-3 is from the low marsh thickly vegetated with *T. maritima* and *S. virginica*.

Samples from two intertidal transects along the Niawiakum River (Nl and Nu) were analyzed in addition to the intertidal samples from the open bay. Transect Nl extends from the channel floor to the transition from marsh to forested upland in the lower Niawiakum River valley (Figure 1, 2). The channel floor is approximately 3.5 m below MLLW, and the marsh-upland transition is estimated at 3.4 m above MLLW. Sampling station Nl-1 is just below MLLW on a steep part of the channel bank thickly vegetated with *Zostera marina*. Nl-2 is on an unvegetated area of the channel bank, and sparse *Z. nana* is growing at the level of sampling station Nl-3. Nl-4 is on a steep marsh scarp vegetated with *Salicornia virginica* and rare *Triglochin maritima*. Nl-5, Nl-6, and Nl-7 are on a gently-sloping high marsh surface, and dominant macrophytes are *Distichlis spicata* and *Salicornia virginica* at Nl-5, and *Deschampsia caespitosa* and *Potentilla pacifica* at Nl-6 and Nl-7. Nl-8 is at the landward edge of the marsh, vegetated by *Carex obnata* and *Achillea* sp.

Transect Nu extends from the channel floor to the highest part of a brackish marsh in the upper Niawiakum River valley (Figures 1, 3). The floor of the channel is graded to near MLLW, and the highest part of the marsh is estimated at 3.2 m above MLLW. Sampling station Nu-1 is on the unvegetated lower part of the channel bank. Nu-2 is just below the lower limit of vegetation. Nu-3 is on the steep marsh scarp vegetated with *Carex*

Transect NI - lower Niawiakum River

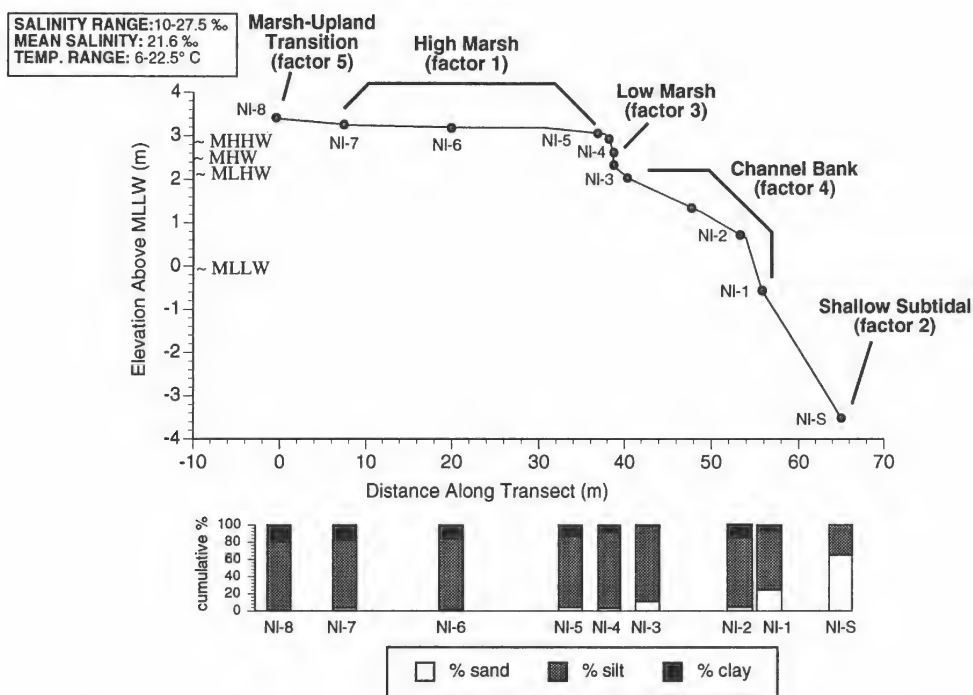


Figure 2. Profile along transect NI, on the lower Niawiakum River. Grain size, salinity, and temperature measurements are for 1990; estimated error for tidal datums is ± 0.10 m.

lyngbei and rare *Triglochin maritima*. Nu-4 is near MHHW, and dominant macrophytes are *Distichlis spicata* and *Deschampsia caespitosa*, with rare *C. lyngbei*. Nu-5, Nu-6, and Nu-7 are on the gently sloping marsh surface where the dominant macrophytes are *D. caespitosa* and *Potentilla pacifica*; Nu-8 is at the highest point on the marsh where the dominant macrophytes are *Juncus balticus* and *P. pacifica*.

Relative elevations along transects Nu and NI were measured with a self-leveling level, which is accurate to ± 1 cm for both horizontal and vertical distances. Tidal datums (Figures 2, 3) were estimated to be within ± 10 cm based on 6 observations of water levels at high and low tides during good weather, and comparison with tidal charts corrected for tidal variation in the estuary (Pacific County Planning Department, written comm., 1990). Diatom and grain-size samples were collected, and dominant macrophytes were

recorded, in April 1990 at eight sampling stations along each transect. Additional diatom samples were collected at the stations in July, September, and December 1990 to test for seasonal variation in diatom distributions. Preliminary analyses showed that relative abundances of species varied among samples collected during different times of the year, but distributions remained constant throughout the year. Therefore, the seasonal counts were combined for this report. Samples from the shallow subtidal channel of the Niawiakum River were collected by using a small dredge deployed from a canoe during low tide.

Diatom samples consisted of about 1 cm^3 of the uppermost 1-2 mm of surface sediment, scraped with a small spatula from and placed in buffered 2% formaldehyde in a glass vial. All modern intertidal surface samples collected in Willapa Bay contained abundant diatoms, some exceeding 5×10^5 cells/cm³. Many of the most prolific species,

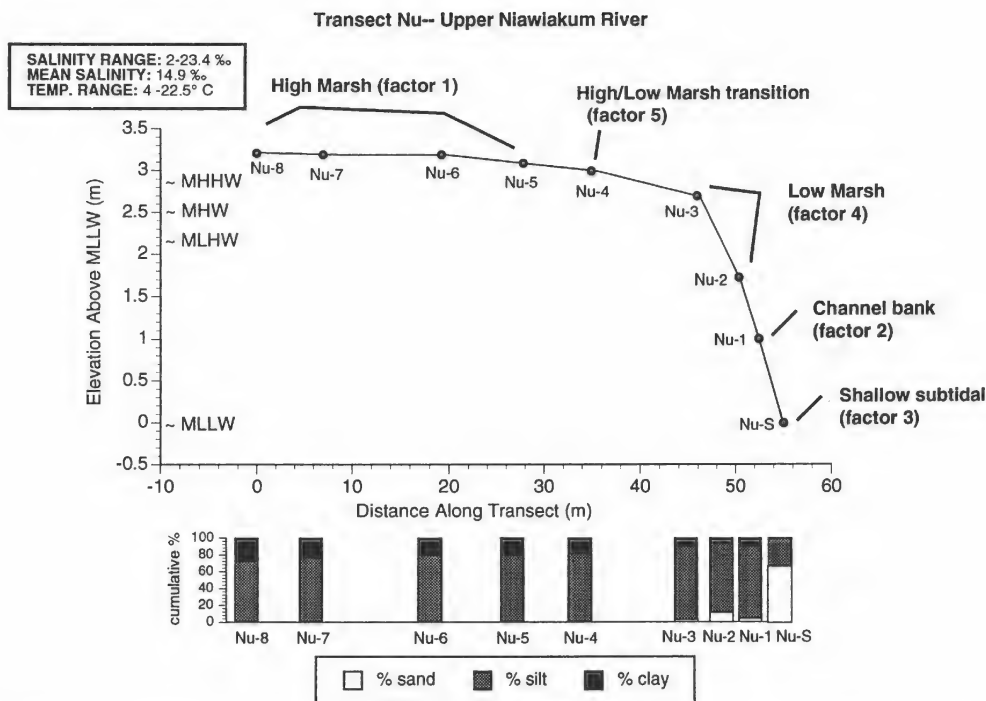


Figure 3. Profile along transect Nu on the upper Niawiakum River. Grain size, salinity, and temperature measurements are for 1990; estimated error for tidal datums is ± 0.10 m.

however, are delicate (e.g., small *Navicula* and *Achnanthes*) and have little chance of surviving in the fossil record. The disparity between the types of marine planktonic diatoms observed in productive surface waters (e.g., *Chaetoceros* spp., *Skeletonema* spp.) and taxa that actually survive dissolution and burial to become fossils (e.g., *Thalassionema* spp. and *Coscinodiscus* spp.) is well known. The same applies to benthic estuarine diatoms, such that many of the most prolific taxa make poor fossils (e.g., *Melosira* spp. and *Synedra* spp.), whereas some of the rarer diatoms in modern deposits (*Caloneis* spp., *Campylodiscus* spp.) may become, by virtue of their resilience to destruction, dependable fossils. Therefore, the factor analysis focused on the modern distributions of 84 diatom taxa that were also observed in Holocene fossil deposits around Willapa Bay (Hemphill-Haley, 1993a and unpub. data).

Macrophyte samples were also collected for qualitative assessment of epiphytic populations: references to an epiphytic life form for individual

species are based on these observations and the detailed analyses by Whiting (1983) and Main and McIntire (1974). Diatoms collected in the field (excluding Toke Point samples that dried out) were stained for evidence of intact cytoplasm with Fast Green FCF cytoplasm stain in buffered 2% formaldehyde, and mounted according to the Taft Syrup Mount (TSM) method (Taft, 1978; Stevenson, 1984). The refractive index of the TSM is sufficient for resolving the valve characteristics of most diatoms, although the fine structure of some delicate species (which are typically absent in fossil deposits) may not be resolvable. Stained samples can be rinsed, dried onto a cover slip, and mounted with Hyrax, which improves resolution of valve characteristics.

At least 400 diatom valves were counted at 625x along random vertical traverses near the middle of the cover slip, with magnifications increased to 1250x to examine smaller specimens (Hemphill-Haley, 1993a). Intact frustules were counted as two valves. For the factor analysis, total counts of

live plus empty frustules and single valves were used to allow for occurrences of both autochthonous and probable allochthonous diatoms, as would naturally occur in fossil assemblages. References to the relative abundances of diatoms are based on the percentage of each species relative to the total number of diatoms counted in each sample, normalized by dividing several dominant species (*Melosira moniliformis*, *M. nummuloides*, *Synedra fasciculata*, and *Paralia sulcata*) by an arbitrary factor of 10: very rare = < 2 %; rare = 2-4.9%; frequent = 5-9.9%; common = 10-33%; abundant = > 33%.

Grain size analyses of Nu, NI, BC, and BR samples were completed with a Cimax Hydrophotometer and Rapid Settling Analyzer (RSA).¹ Calibration tests indicate that the hydrophotometer is precise to $\pm 3\%$ and the RSA to $\pm 5\%$ (Torresan, 1987). Sediment textures SP and TP samples were estimated in the field. Water temperature and salinity data along transects Nu and NI were collected from the adjacent channel near the surface at high tide using a YSI Model 33 S-C-T meter with reported accuracies of $\pm 0.5^\circ\text{C}$ and ± 0.5 ppm, respectively. Salinity data for the open bay were provided by the Washington Department of Fisheries Laboratory at Nahcotta. Data used for this study (diatom counts and taxonomy, grain-size results) are also available in U.S. Geological Survey Open-File Reports (Hemphill-Haley, 1993a, b).

Statistics

The program CABFAC was used to generate a Q-mode factor analysis (Klovan and Imbrie, 1971) to identify end-member groups of surface samples from three data sets: (1) transect NI; (2) transect Nu; and (3) the four sampling localities bordering the open bay. Variables for the factor analysis consist of 84 taxa observed in the modern samples that were likewise observed in fossil samples from Willapa Bay. Some varieties of species were included with the nominate forms where both were observed to commonly co-occur, including varieties of *Achnanthes brevipes*, *A. hauckiana*, *A. lanceolata*, *Frustulia vulgaris*, and *Navicula lyra*. The *Actinopterychus* spp. group includes *A. senarius* and *A. splendens*, and the *Odontella* spp. group includes

O. aurita and *O. obnuta*. Small forms of *Paralia sulcata* (less than 20 μm diameter) were counted separately from large forms because of evidence that valve size may be ecologically controlled (Roe-lofs, 1984) and observations that small forms are more widely distributed in lower-salinity areas of the estuary (Hemphill-Haley, 1993a).

The results of the factor analysis are based on the relative abundances of diatom taxa in each sample. Beginning with the raw census-data matrix [X] of n entities (i.e., samples) and m variables (i.e., taxa), value counts were transformed to the percentage of the range of total numbers for each variable, thereby giving as much weight to rare species with limited distributions as to common species that are particularly dominant in certain localities. The varimax rotation method was used to simplify the interpretation of factor loadings (i.e., the contributions of each sample to the factors). The varimax factor-loading and factor-score matrices provided by CABFAC list the contributions of each sample and each taxon to the factors, respectively. Taxa with the highest factor scores are indicative of the modern environment in which they are found either because of their restricted distribution or their particular abundance in that environment. The factor assemblages in this report include both autochthonous and suspected allochthonous species and show the influence of resuspension and mixing of diatom assemblages in the intertidal zone. For the analyses, the lowest number of factors explaining at least 75% of the variance was used. The sharp break from relatively high to low factor scores was used to separate important from extraneous taxa comprising each factor.

Results

Lower Niawiakum transect (NI)

Salinities ranged from 10‰ to 27.5‰ at transect NI, with a mean of 21.6‰ (Figure 2). A five-factor model (Figure 4) identified the marsh-upland transition (NI-8; Factor 5), high marsh (NI-5 to NI-7; Factor 1), low marsh (NI-4; Factor 3), channel bank (NI-1 to NI-3; Factor 4), and shallow channel (NI-S; Factor 2). Of the 84 species and groups considered in this study, 77 were observed along this transect, and 57 scored high in the factor analysis. The five-factor model explains 78% of the total variance, or 88% of the data (Table 1).

Marsh-upland transition—Factor 5 (Figure 4e). Important autochthonous diatoms include *Denticula*

¹Any use of trade, product, or firm names in this report is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Transect NI: Factor Scores

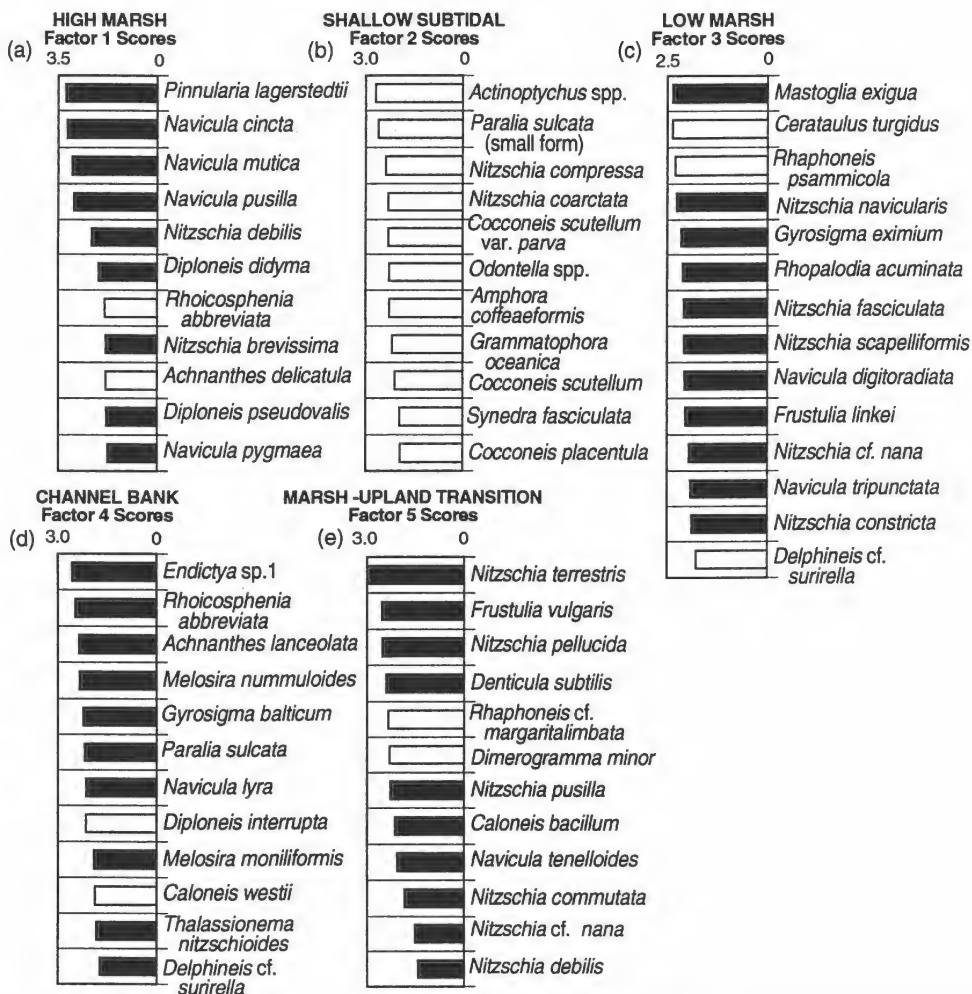


Figure 4. Factor scores along transect NI for autochthonous species (black bars) and suspected allochthonous species (white bars).

subtilis, *Nitzschia pusilla*, and *Navicula tenelloides*. *Nitzschia terrestris* was rare but scored high in the factor analysis because of its limited distribution. *Nitzschia commutata*, *Frustulia vulgaris*, *Caloneis bacillum*, *Nitzschia cf. nana*, and *Nitzschia debilis* are found in both low and high marshes. Allochthonous diatoms include very rare valves of *Raphoneis cf. margaritalimbata* and *Dimerogramma minor*.

High marsh—Factor 1 (Figure 4a). Autochthonous diatoms that can be used to define the high marsh include *Pinnularia lagerstedtii*, *Navicula pusilla*, and *Nitzschia brevissima*. *Navicula cincta*, *Navicula mutica*, *Diploneis pseudovalis*, *D. didyma*, and *N. debilis* are distributed in high and low marshes. Allochthonous diatoms include very rare valves of *Rhoicosphenia abbreviata* and *Achnanthes delicatula*. *Navicula pygmaea* is also very rare, and its significance is uncertain.

TABLE 1. Factor loadings for sampling stations along transect N1 on the lower Niawiakum River. Boldface numbers denote defining factors for each sampling station.

Station	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
N1-S	0.884	0.077	0.925	0.021	-0.121	-0.086
N1-1	0.669	-0.002	0.616	0.112	-0.515	-0.111
N1-2	0.747	0.146	0.180	-0.025	-0.832	-0.029
N1-3	0.529	0.094	0.457	0.258	-0.472	-0.148
N1-4	0.781	0.155	0.090	0.860	-0.039	-0.086
N1-5	0.769	0.658	-0.049	0.108	-0.291	-0.487
N1-6	0.874	0.919	0.069	0.135	-0.081	0.000
N1-7	0.804	0.820	0.046	0.090	-0.024	-0.347
N1-8	0.925	0.278	0.181	0.080	-0.056	-0.897
variance		23.186	16.963	9.61	14.344	13.477
cumulative variance		23.186	40.148	49.759	64.103	77.58

Low marsh—Factor 3 (Figure 4c). Autochthonous diatoms that identify the low marsh include *Gyrosigma eximium* (common to abundant), *Nitzschia navicularis*, *Nitzschia scalpelliformis*, and *Frustulia linkei*. *Mastogloia exigua* may be primarily a low-marsh species, but it was also observed on the adjacent channel bank (N1-3). It is frequent in low-marsh samples from Toke Point. *Rhopalodia acuminata*, *Navicula digitoradiata*, and *Nitzschia constricta* are found in both low marshes and adjacent flats, and *Nitzschia fasciculata* and *N. cf. nana* are found in low and high marshes. Allochthonous diatoms include very rare valves of *Cerataulus turgidus*, *Rhaphoneis psammicola*, and *Delphineis cf. surirella*.

Channel bank—Factor 4 (Figure 4d). Autochthonous channel-bank diatoms include *Melosira moniliformis*, *M. nummuloides*, and *Paralia sulcata*; *Gyrosigma balticum*, *Navicula lyra*, and *Endictya* sp. 1 (Hemphill-Haley, 1993b) are rare but scored high in the factor analysis because of their limited distribution. *R. abbreviata* and *Achnanthes lanceolata* are indicative of channel banks in less saline areas of northern Willapa Bay (Hemphill-Haley, 1993a), and may indicate periods of low-salinity runoff at this site. *Thalassionema nitzschioides* is a widely distributed marine neritic diatom (Cupp, 1943), but was also recorded by McIntire and Overton (1971) in attached lower intertidal samples in Yaquina estuary (Oregon). Allochthonous diatoms probably include rare valves of *Diploneis interrupta*, which was frequent in the transitional marsh at transect

Nu, and rare valves of *Caloneis westii*, which was frequent in the low marsh at Toke Point and Stony Point.

Shallow subtidal zone—Factor 2 (Figure 4b). By definition, all diatoms from the high-energy river channel are allochthonous (Vos and de Wolf, 1988). Species that scored high in the factor analysis consist of lower-intertidal epiphytes (*Grammatophora oceanica*, *Cocconeis scutellum*, *C. scutellum* var. *parva*, *Synedra fasciculata*), epipelion (*Nitzschia compressa*, *Nitzschia coarctata*, *Cocconeis placentula*), or tychoplanktonic diatoms (ie., both benthic and planktonic—*Actinoptychus* spp., *P. sulcata* (small form), and *Odontella* spp.).

Upper Niawiakum transect (Nu)

Salinities ranged from 2‰ to 23.4‰ at transect Nu, with a mean of 14.9‰ (Figure 3). A five-factor model (Figure 5) identified the high marsh (Nu-5 to Nu-8; Factor 1), low-to-high transitional marsh (Nu-4; Factor 5), low marsh (Nu-2, Nu-3; Factor 4), channel bank (Nu-1; Factor 2) and channel floor (Nu-S; Factor 3) (Figure 2). Of the 84 species and groups considered in this study, 73 were observed along this transect, and 58 scored high in the factor analysis. The five-factor model explains 83% of the total variance, or 91% of the data (Table 2).

High marsh—Factor 1 (Figure 5a). Autochthonous diatoms indicative of the high marsh include *P. lagerstedtii*, *N. pusilla*, *D. subtilis*, *N. tenelloides*, *N. debilis*, and *Nitzschia pellucida*. *N. mutica*,

Transect Nu: Factor Scores

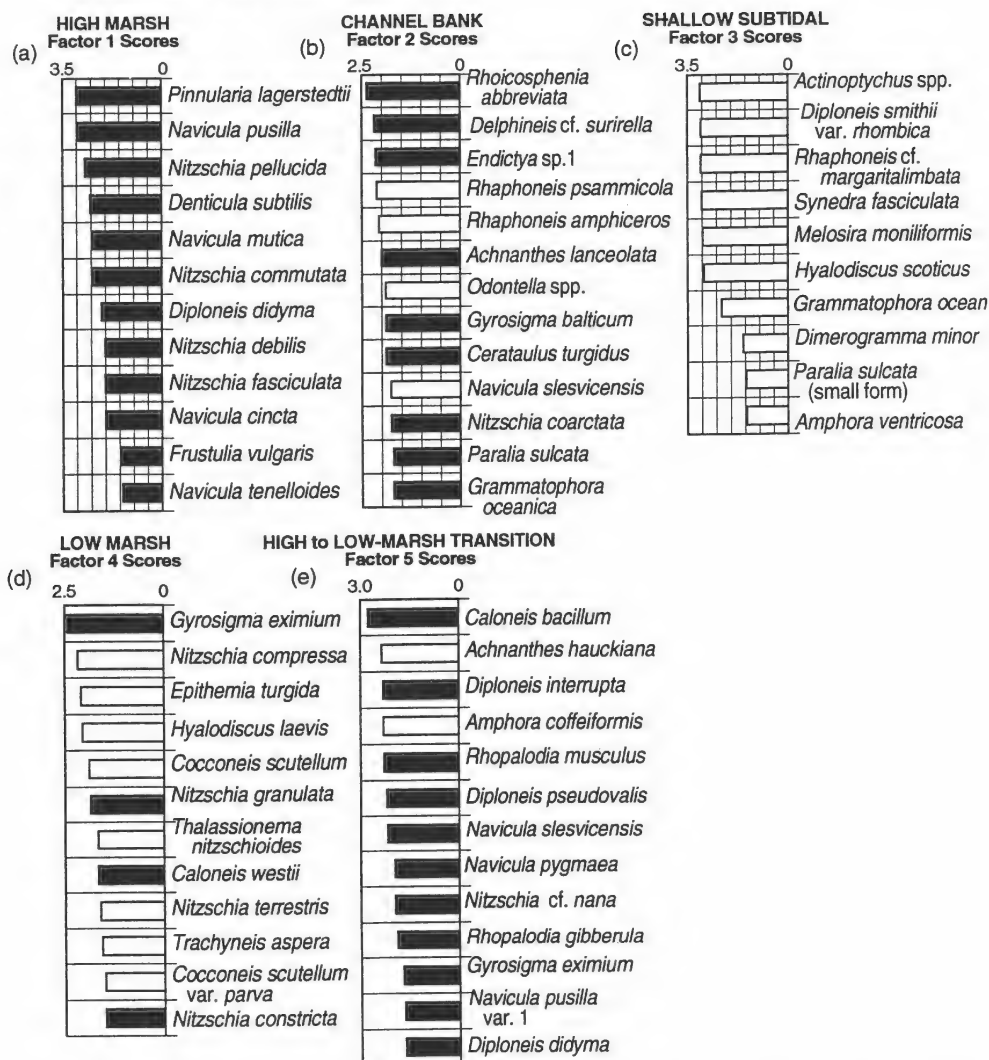


Figure 5. Factor scores along transect Nu for autochthonous species (black bars) and suspected allochthonous species (white bars).

N. cincta, *N. commutata*, *N. fasciculata*, *Diploneis didyma* and *Frustulia vulgaris* are distributed in high and low marshes.

Low-to-high transitional marsh—Factor 5 (Figure 5e). Sampling station Nu-4 is positioned near MHHW where it experiences substantially more tidal submergence than the high marsh stations and somewhat more emergence than stations lower on

the transect. Autochthonous diatoms include *C. bacillum* and *D. pseudovalis*, which were abundant at Nu-4 but also observed in high-marsh samples. *D. interrupta* totaled 3.4% of the assemblage at sampling station Nu-4, but was less than 1% in other marsh samples; *D. didyma*, *N. cf. nana*, and *Navicula pusilla* var. 1 are distributed in low and high marshes. *G. eximium* and *Rhopalodia*

TABLE 2. Factor loadings for sampling stations along transect Nu on the upper Niihau River. Boldface numbers denote defining factors for each sampling station.

Station	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Nu-S	0.974	0.032	0.143	-0.970	-0.110	0.002
Nu-1	0.888	0.038	0.875	-0.196	-0.265	0.109
Nu-2	0.871	0.076	0.127	-0.204	-0.888	0.136
Nu-3	0.801	0.295	0.435	0.090	-0.714	0.087
Nu-4	0.922	0.312	0.186	0.013	-0.138	0.878
Nu-5	0.710	0.628	-0.145	-0.038	-0.198	0.504
Nu-6	0.740	0.751	-0.070	-0.043	-0.322	0.255
Nu-7	0.768	0.826	0.197	-0.090	-0.107	0.167
Nu-8	0.821	0.892	0.099	0.052	0.064	0.091
variance		29.215	12.233	11.588	17.319	12.946
cumulative variance		29.215	41.449	53.037	70.356	83.302

musculus were rare in these samples. Allochthonous diatoms include very rare valves of *Achnanthes hauckiana* and *Amphora coffeaeformis*.

Low marsh—Factor 4 (Figure 5d). Autochthonous species indicative of the low marsh include *G. eximium*, *Nitzschia granulata*, *C. westii*, and *N. constricta*. Allochthonous diatoms include very rare valves washed in from the adjacent muddy bank (*N. compressa*, *Epithemia turgida*, *Hyalodiscus laevis*, and *Trachyneis aspera*, *T. nitzschoides*) or high marsh (*N. terrestris*). Primarily empty frustules of *C. scutellum* and *C. scutellum* var. *parva* may also be allochthonous.

Channel bank—Factor 2 (Figure 5b). Autochthonous diatoms include *P. sulcata*, *G. oceanica*, *D. cf. surirella*, *N. coarctata*, *G. balticum*. Other possibly autochthonous, but very rare, diatoms include *Endictya* sp. 1, *C. turgidus*, *R. psammicola*, *R. amphicerus*, and *Odontella* spp. *R. abbreviata* and *A. lanceolata* are likewise distributed on the channel bank along transect N1. Allochthonous diatoms include very rare valves of *Navicula slesvicensis*, which is a high marsh species at Stony Point.

Shallow subtidal—Factor 3 (Figure 5c). All diatoms from the channel are considered to be allochthonous and include species distributed in lower-intertidal flats and *Zostera* beds. *Diploneis smithii* var. *rhombica* scored high in the factor analysis because of its limited distribution. No live cells were observed in Willapa Bay samples, but this species commonly occurs with *C. westii* in inter-

tidal marshes in the Copper River delta, Alaska (Hemphill-Haley, unpub. data).

Intertidal Samples Fringing the Open Bay

Salinity data for northern Willapa Bay, collected by the Washington Department of Fisheries Laboratory at Nahcotta, indicate typical ranges of 10-30‰, with occasional polyhalobous (>30‰) levels. An eight factor model (Figure 6) identified two sandy-tidal-flat assemblages (BC-1, BC-3; Factor 1; and BC-2; Factor 7), two silty-tidal-flat assemblages (SP-1 to SP-3; Factor 3; and samples BR-1, BR-2; Factor 4), a sandy-tidal-slough assemblage (TP-1; Factor 8), two *Triglochin* low-marsh assemblages (SP-4; Factor 6; and TP-2, TP-3; Factor 2), and a *Potentilla* high-marsh assemblage (SP-5; Factor 5). Of the 84 taxa considered for this study, 70 were observed in these samples, and 68 scored high in the factor analysis. The eight-factor model explains 81% of the variance, or 90% of the data (Table 3).

Sandy tidal flat 1—Factor 1 (Figure 6a): Indicative sandflat species include abundant valves of *C. scutellum* var. *parva* and *A. delicatula*. Other autochthonous species include *Trachysphenia australis*, *Cymatosira belgica*, *Navicula granulata*, *N. cancellata*, and *N. cryptolyra*. Allochthonous diatoms include very rare valves of *C. placentalis*.

Sandy tidal flat 2—Factor 7 (Figure 6g): Sample BC-2 was separated from samples BC-1 and BC-3 in the factor analysis because of the high relative abundances of the autochthonous species *N. lyra*,

Open-Bay Samples: Factor Scores

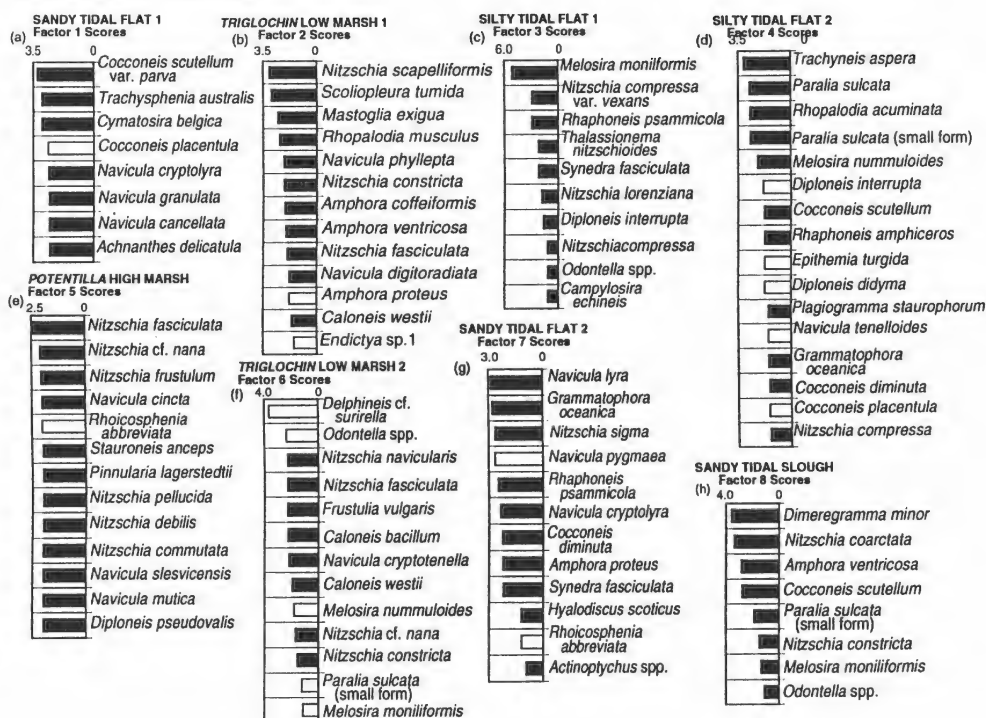


Figure 6. Factor scores of intertidal surface samples collected from the open bay for autochthonous species (by black bars) and suspected allochthonous species (white bars).

TABLE 3. Factor loadings for tidal flat and marsh samples collected from northern Willapa Bay. Boldface numbers denote defining factors for each sampling station.

Sample	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
SP-1	0.806	0.034	0.079	-0.832	0.050	-0.031	0.030	0.215	-0.237
SP-2	0.747	0.039	-0.146	-0.563	-0.153	-0.196	-0.505	-0.029	-0.300
SP-3	0.797	0.032	0.107	-0.833	-0.198	0.143	-0.060	0.027	0.160
SP-4	0.862	0.008	0.252	-0.026	-0.101	0.195	-0.865	0.029	0.025
SP-6	0.937	0.008	0.015	-0.039	-0.011	0.958	-0.104	0.026	-0.074
BR-1	0.775	0.022	-0.035	-0.097	-0.824	-0.061	-0.227	0.131	-0.116
BR-2	0.794	0.143	0.085	-0.064	-0.862	0.085	0.050	0.002	-0.096
BC-1	0.527	0.553	-0.022	0.017	-0.163	-0.044	-0.100	0.349	-0.245
BC-2	0.907	0.123	0.043	-0.182	-0.090	0.036	0.026	0.919	0.043
BC-3	0.896	0.941	0.046	-0.028	-0.046	0.014	0.045	0.007	0.066
TP-1	0.867	0.048	0.291	-0.109	-0.220	0.113	-0.023	-0.033	-0.840
TP-2	0.819	0.055	0.888	-0.064	0.052	-0.051	-0.018	0.127	-0.046
TP-3	0.814	0.029	0.840	-0.060	-0.108	0.078	-0.209	-0.075	-0.194
variance		9.51	13.021	13.643	12.285	8.091	8.695	8.129	7.784
cumulative variance		9.51	22.531	36.174	48.459	56.55	65.244	73.373	81.158

S. fasciculata, *G. oceanica*, and *Hyalodiscus scoticus*, and the restricted occurrence of *Amphora proteus*. *Cocconeis diminuta* and *N. cryptolyra* were observed attached to sand grains. *R. psammicola* was originally described by Riznyk (1973) from tidal flats in Yaquina Bay, Oregon. *Nitzschia sigma*, a cosmopolitan mesohalobous benthic diatom (Hendey, 1964), was very rare at this site. Allochthonous diatoms include very rare valves of *N. pygmaea* and *R. abbreviata*.

Silty tidal flat 1—Factor 3 (Figure 6c): Dominant autochthonous species include *M. moniliformis*, *S. fasciculata*, *Odontella* spp., *Nitzschia compressa* var. *vexans*, *R. psammicola*, *T. nitzschiioides*, *Nitzschia lorenziana*, *N. compressa*, and *Campylodiscus echineis*. Allochthonous diatoms include very rare valves of *D. interrupta*.

Silty tidal flat 2—Factor 4 (Figure 6d): Autochthonous diatoms: *R. acuminata*, *G. oceanica*, and *C. scutellum*. Rare live cells of *Trachyneis aspera* and *Plagiogramma stauraphorum* may be autochthonous, which is consistent with tidal-flat distributions reported elsewhere (Hendey, 1964; Riznyk, 1973; Tynni, 1983). The highest relative percentages of *P. sulcata* (large form) were observed in these samples. Allochthonous diatoms include very rare valves of *D. interrupta*, *D. didyma*, *Epithemia turgida*, *N. tenelloides*, and *C. placentula*, possibly washed onto the tidal flat by the Bone River.

Sandy tidal slough—Factor 8 (Figure 6h): Autochthonous diatoms include species that favor a sandy substrate (*D. minor*, *N. coarctata*, *Amphora ventricosa*), are epiphytic on *Zostera* (*C. scutellum*, *M. moniliformis*), or are generally distributed on tidal flats (*N. constricta*, *Odontella* spp., *P. sulcata*).

Triglochin low marsh 1—Factor 2 (Figure 6b): Autochthonous diatoms include common valves of *M. exigua*, plus *Rhopalodia musculus*; *N. scalpelliformis*, *Navicula phyllepta*, *N. digitoradiata*, *C. westii*, and *Amphora coffeaeformis*. *Scoliopleura tumida*, *A. ventricosa*, and *N. constricta* are rare but probably autochthonous. Allochthonous diatoms: very rare valves of *Amphora proteus* and *Endictya* sp. 1, which may have been washed in from the adjacent tidal slough.

Triglochin low marsh 2—Factor 6 (Figure 6f): Autochthonous species indicative of the low marsh include common cells of *C. westii*, *C. bacillum*, *N.*

constricta, *N. cf. nana*, and *Navicula cryptotenella*. Rare valves of *N. navicularis*, *N. fasciculata*, and *F. vulgaris* are probably also autochthonous. Allochthonous diatoms include very rare valves of *D. cf. surirella*, *Odontella* spp., *M. nummuloides*, *M. moniliformis*, and *P. sulcata* (small form).

Potentilla high marsh (Factor 5; Figure 6e): Autochthonous diatoms include common cells of *Navicula slesvicensis*, *N. mutica*, and *Stauroneis anceps*, and frequent cells of *P. lagerstedtii*, *N. commutata*, *N. pellucida*, and *N. cf. nana*. *N. cincta*, *N. debilis*, and *D. pseudovalis*, also observed in marsh samples from transects N1 and Nu, were rare at this locality. Allochthonous diatoms include very rare valves of *R. abbreviata*.

Discussion

The distributions of intertidal diatoms in southwestern Washington reflect the three-tiered intertidal zonation driven by differing amounts of tidal submergence, similar to the distributions of marsh macrophytes (Macdonald, 1977a, b; Frey and Basan, 1985; Sayce, 1988) and benthic foraminifers (Jennings and Nelson, 1992). The 84 taxa discussed in this report show variable affinities for different parts of the intertidal and shallow subtidal zone in northern Willapa Bay (Figure 7). Many species are distributed in more than one zone, whereas others are more restricted. The sampling interval in this study did not clearly differentiate the boundaries between intertidal zones, but as shown by Jennings and Nelson (1992) and Nelson and Kashima (1993), these boundaries may be transitional over several tens of centimeters. Although the factor analysis separated shallow-subtidal from lower-intertidal-channel-bank samples, the shallow-subtidal samples predominantly contain allochthonous diatoms from lower intertidal flats and channel banks, and thus it could be argued that lower-intertidal and shallow-subtidal fossil assemblages would be indistinguishable. There is some indication that deeper channels (>4 m deep) may be distinguishable from shallow subtidal channels in Willapa Bay by higher planktonic diatom/benthic diatom ratios (Hemphill-Haley, unpub. data), but this requires further investigation.

Overlapping salinities among the transects and open-bay localities allowed for similar diatom assemblages in ecological zones at different sites. This agrees with published observations of broad salinity ranges for many brackish species, with dramatic

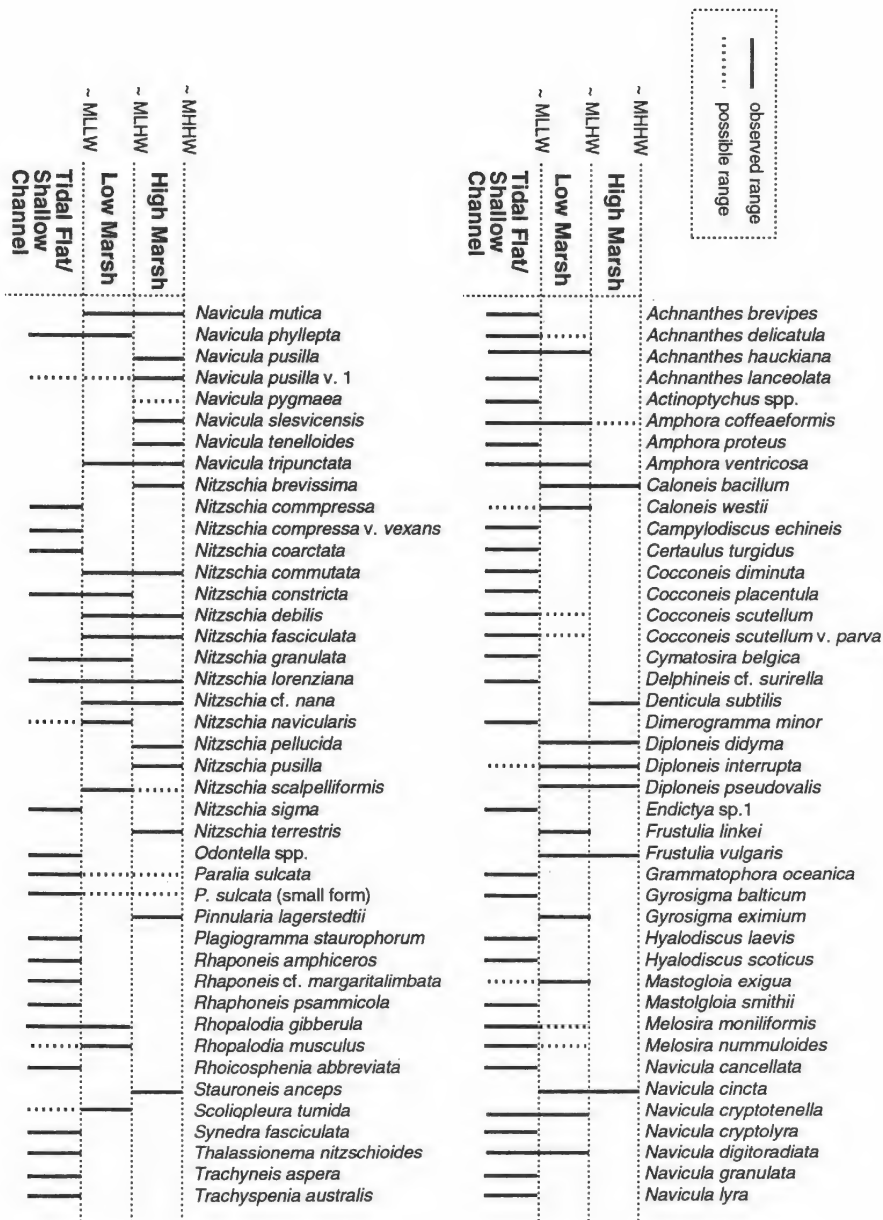


Figure 7. Intertidal ranges for 84 diatom species and groups from northern Willapa Bay. Solid lines, dominant range; dashed lines, possible range indicated by rare occurrences. Absolute elevations for the intertidal zones are not indicated because these elevations are constrained by local tidal range and vary with location in an estuary.

shifts in diatom populations (triggered by the osmotic capabilities of various taxa) occurring at salinities either below 5‰ or above 30‰ (Moore and McIntire, 1977; McIntire, 1978; Amspoker and McIntire, 1978; Vos and de Wolf, 1988; Hemphill-Haley, 1993a). However, lower average salinities at transect Nu, higher amounts of fresh-water run-off from the Pleistocene terrace at Stony Point, and geomorphic differences between the low-marsh zones of the open bay and Niawiakum River may have contributed to some differences among diatom populations in this study. Muddy banks of the river and silty intertidal flats of the open bay were dominated by prolific species such as *Paralia sulcata*, *Melosira moniliformis*, *Synedra fasciculata*, and *Grammatophora oceanica*. The open bay sand flats, however, hosted assemblages that were distinct from the muddy epipellic assemblages. Several species that are commonly observed in late Holocene deposits (particularly *Caloneis westii*, *Scoliopleura tumida*, *Navicula digitoradiata*, and *Campylodiscus echineis*; Hemphill-Haley, unpub. data) were either rare or absent in the steep low marsh zone along the river, but were frequent in the gently sloping, thickly vegetated, *Triglochin*-dominated low marshes of the open bay. Several small, sturdy species (e.g., *Pinularia lagerstedtii*, *Navicula pusilla*, *N. mutica*, *Denticula subtilis*) appear to be reliable for identifying the high marsh, particularly *Deschampsia*-dominated high marshes.

The factor analysis identified a subzone at the marsh-upland transition because of the higher concentration of certain species (e.g., *D. subtilis*, *N. pusilla*) in that area. Regardless of whether a particular fossil assemblage can be recognized, the marsh-upland transition can be identified by the disappearance of diatoms in samples deposited above EHW. Unless standing water is present (which I observed only once during reconnaissance surveys in various areas of Willapa Bay), upland surfaces above the range of highest tides bordering estuarine marshes in southwestern Washington do not support diatom populations, including freshwater species (see also Nelson and Kashima, 1993). Therefore, the position of paleo-EHW can be identified by the transition from peaty diatom-rich marsh deposits to upland peats barren of diatoms.

The amount of submergence or desiccation at different intertidal elevations is reflected in the physiology of the diatom species that inhabit differ-

ent intertidal zones and influences how well a fossil record is preserved. For example, the high-marsh diatoms observed in this study are dominated by small, solitary, heavily silicified species that are tolerant of large fluctuations in temperature, salinity, and periods of desiccation imposed by the higher elevation of the marsh environment (e.g., *D. subtilis*, *P. lagerstedtii*, *N. pusilla*). For example, the diurnally submerged bank and low marsh along transect NI experienced average water temperatures that ranged from 20.5°C in July 1990 to 5.9°C in December 1990. In contrast, the high marsh was desiccated at air temperatures of 25.5°C in July 1990 and frozen in December 1990, yet abundant live diatoms were obtained in surface samples on both occasions, attesting to the resilience of the species observed there. Many of these species can be expected to fossilize well, in contrast to some low-marsh diatoms that undergo tidal submergence at least once per day and are more delicately silicified or live in gelatinous tubes (e.g., *G. eximium*, *N. scalpelliformis* (Williams, 1965)).

Substrate and sediment grain size are strong controlling factors in the distribution of benthic estuarine diatoms (e.g., McIntire and Moore, 1977; Amspoker and McIntire, 1978; Whiting, 1983; Whiting and McIntire, 1985; Kosugi, 1987). The propensity for organic carbon to accumulate in fine grained or poorly sorted silty sediment, as opposed to well-sorted sandy deposits, influences the distribution of intertidal diatoms. In general, diatoms are more abundant on silty tidal flats than on sandy tidal flats (Colijn and Dijkema, 1981; Laws, 1988) if they are not dominated by other organisms (Riznyk and Phinney, 1972). Therefore, finer grained paleoestuarine deposits can be expected to be more diatomaceous than sandy deposits, even excluding the effects of winnowing. In addition, diatoms are typically more abundant where certain macrophytes are present—either to trap fine-grained sediment or to act as substrate for epiphytes—than where they are absent (Round, 1971; Main and McIntire, 1974; McIntire and Moore, 1977). On the channel banks and tidal flats in Willapa Bay, epiphytes are prolific on *Zostera*, especially *M. moniliformis*, *M. nummuloides*, and *S. fasciculata*. However, these large, delicate species leave a poor fossil record. Although solitary species on silty flats (e.g., *Nitzschia acuminata*, *C. echineis*) are far less prolific than epiphytes on *Zostera*, they are much more likely to survive fossilization.

Transport and redeposition of diatom frustules in coastal areas cannot be ignored in biostratigraphic studies (e.g., Beyens and Denys, 1982; Vos and de Wolf, 1988; 1993). In this study, virtually all modern samples contained suspected allochthonous diatom valves, indicating what could be expected for fossil deposits. Spring high tides, particularly in association with storm surges, are capable of topping the highest marshes in Willapa Bay and scattering diatom frustules across upland surfaces. During typical weather conditions, many sediment-associated diatoms, especially such large chain-forming taxa as *Melosira* or *Paralia* that cannot withstand strong water turbulence, will readily be lifted into the plankton. Whiting (1983) likewise noted occurrences of benthic species in plankton samples.

With each rising tide, epipellic diatoms that fail to withdraw below the sediment surface may be lifted up and transported up estuary as a surface "film." Casual observation showed that most diatoms in the surface film are small, delicate epipellic species (e.g., *Navicula halophila* group; Hemphill-Haley, 1993b) that are not well represented in fossil deposits. Excluding the effects of localized differences in sediment texture causing patchy diatom distributions, this regular mixing and reseeded by tides results in a generally homogeneous lower intertidal zone (see Riznyk and Phinney, 1972; Riznyk, 1973; Amspoker and McIntire, 1978).

However, although diatom cells can be assumed to be redeposited on a regular basis in any estuary, observations of the modern Willapa Bay samples indicates that autochthonous benthic species typically far outnumber suspected allochthonous benthic species. Thus, this suggests that in most cases (assuming good preservation) it should be possible to reconstruct the depositional environment of a fossil deposit based on its autochthonous constituents. Sullivan (1975) noted that live allochthonous cells did not survive and reproduce in intertidal habitats for which they were physiologically unsuited, further suggesting that redistributed diatoms are unlikely to completely mask *in situ* assemblages associated with particular intertidal settings. Therefore, although allochthonous cells will almost certainly be present in a sample, it is reasonable to expect that the depositional setting of a fossil deposit may be inferred based on its autochthonous components.

Using the results of the factor analysis as an example of what can be expected in fossil deposits, allochthonous diatoms are present in most samples, with fewer allochthonous valves in high-marsh deposits and more frequent allochthonous valves in low-marsh and tidal-flat samples. Thus, because of the occurrences of allochthonous valves, low marshes and tidal flats and banks may be more difficult to recognize on the basis of diatom assemblages, unless autochthonous valves are dominant and/or better preserved (i.e., show evidence for being *in situ*).

Staining the diatom samples used for this study provided valuable insight into the distributions of modern estuarine species (see also Kosugi, 1987). Although acid cleaning removes organic material that may obscure the ornamentation on some valves, it prohibits the identification of cells that were live or recently deceased at the time of collection. Although epilithic or epiphytic samples can be assumed to be *in situ* (e.g., McIntire and Overton, 1971; Main and McIntire, 1974; Moore and McIntire, 1977), sediment-associated diatoms found on tidal flats and salt marshes may or may not be in place, and once a sample is cleaned it is impossible to discern whether or not a species was a living part of the assemblage (e.g., Riznyk, 1973; Tynni, 1986). Although identifying a live cell does not guarantee that it is autochthonous (as live cells of such easily transported species as *P. sulcata* were commonly observed), recognizing the extent of probable allochthonous input provides the kind of information necessary for improving paleoecological interpretations which ultimately must be based on co-occurrences of autochthonous and allochthonous taxa.

Conclusions

Diatoms were collected in surface sediment samples from tidal flats, intertidal channel banks, shallow subtidal channels, and low and high marshes in northern Willapa Bay, Washington. Diatom frustules were stained in order to identify possible allochthonous taxa in various ecologic settings. Q-mode factor analyses identified groups of intertidal samples composed of comparable diatom assemblages; although autochthonous species dominate, some allochthonous species also scored high in the factor analysis indicating the regular influence of reworking in the estuary and the prevalence of a mixed biocoenosis/thanatocoenosis in potential fossil deposits.

The results suggest that diatoms can be used to identify three environmental zones relative to tidal level: (1) tidal flats, channel banks, and shallow subtidal channels below MLHW; (2) low marshes between MLHW and MHHW; and (3) high marshes between MHHW and EHW. In some places, an additional zone may be recognizable on the basis of assemblages that thrive near EHW at the marsh-upland transition, but the position of paleo-EHW is also identifiable by the disappearance of diatoms in samples deposited above EHW. The absolute elevations of intertidal zones depend on the local tidal range, which varies within a large estuary such as Willapa Bay.

Because many of the species observed in this study have cosmopolitan distributions, these data are probably applicable to Quaternary estuarine paleoecological studies in other temperate areas of the world, as well as throughout the coastal Pacific Northwest.

Literature Cited

- Admiraal, W., 1979. Salinity tolerance of benthic estuarine diatoms as tested with a rapid polarographic measurement of photosynthesis. *Mar. Biol.* 39: 11-18.
- Amspoker, M.C., and C.D. McIntire, 1978. Distribution of intertidal diatoms associated with sediments in Yaquina Estuary, Oregon. *J. Phycol.* 14: 387-395.
- Atwater, B.F., 1987. Evidence for great Holocene earthquakes along the outer coast of Washington state. *Science* 236: 942-944.
- . 1988. Subduction-earthquake telltales beneath coastal lowlands. P. 157-162 in A.J. Crone and E.M. Omdahl (eds.), *Directions in Paleoseismology: Proceedings of Conference XXXIX*. U.S.G.S. Open-File Rep. 87-673.
- . 1992. Geologic evidence for earthquakes during the past 2000 years along the Copalis River, southern coastal Washington. *J. Geophys. Res.* 97(B2): 1901-1919.
- Atwater, B.F., M. Stuiver, and D.K. Yamaguchi, 1991. Radiocarbon dating and subduction-earthquake magnitude along the Washington coast, northwestern United States. *Nature* 353: 156-158.
- Atwater, B.F., and D.K. Yamaguchi, 1991. Sudden, probably coseismic submergence of Holocene trees and grass in coastal Washington state. *Geol.* 19(7): 706-709.
- Beyens, L., and L. Denys, 1982. Problems in diatom analysis of deposits: Allochthonous valves and fragmentation. *Geol. Mijnb.* 61: 159-162.
- Bucknam, R.C., E. Hemphill-Haley, and E.B. Leopold, 1992. Abrupt uplift within the past 1700 years at southern Puget Sound, Washington. *Science* 258: 1611-1614.
- Castenholz, R.W., 1963. An experimental study of the vertical distribution of littoral marine diatoms. *Limnol. Oceanogr.* 8(4): 450-462.

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- Clague, J.J., and Bobrowsky, P.T., 1994. Evidence for a large earthquake and tsunami 100-400 years ago on western Vancouver Island, British Columbia. *Quat. Res.* 41: 176-184.
- Clarke, S.H., Jr., and G.A. Carver, 1992. Late Holocene tectonics and paleoseismicity, southern Cascadia subduction zone. *Science* 255: 188-192.
- Colijn, F., and K.S. Dijkema, 1981. Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. *Mar. Ecol. Prog. Ser.* 4: 9-21.
- Cupp, E.E., 1943. *Marine Plankton Diatoms of the West Coast of North America*. University of California Press, Berkeley and Los Angeles.
- Darizeno, M.E., and C.D. Peterson, 1990. Episodic tectonic subsidence of late Holocene salt marshes, Northern Oregon Central Cascadia Margin. *Tectonics* 9(1): 1-22.
- Eronen, M., T. Kankainen, and M. Tsukada, 1987. Late Holocene sea-level record in a core from the Puget Lowland, Washington. *Quat. Res.* 27: 147-159.
- Frey, R.W., and P.B. Basan, 1985. Coastal Salt Marshes. P. 101-169 in R. A. Davis Jr. (eds.), *Coastal Sedimentary Environments*. Springer-Verlag, New York.
- Hemphill-Haley, E., 1993a. Occurrences of recent and Holocene intertidal diatoms (Bacillariophyta) in northern Willapa Bay, Washington. U.S.G.S. Open-File Rep. 93-284.
- . 1993b. Taxonomy of recent and fossil (Holocene) diatoms (Bacillariophyta) from northern Willapa Bay, Washington. U.S.G.S. Open-File Rep. 93-289.
- Hendey, N.I., 1964. *An Introductory Account of the Smaller Algae of British Coastal Waters, Part V: Bacillariophyceae (Diatoms)*. Ministry of Agriculture, Fisheries, and Food, Fishery Investigations Series IV, London.

- Jennings, A.E., and A.R. Nelson, 1992. Foraminiferal assemblage zones in central Oregon salt marshes—relation to marsh floristic zones and sea level. *J. Foram. Res.* 22(1): 13-29.
- Klovan, J.E., and J. Imbrie, 1971. An algorithm and Fortran IV program for large scale Q-mode factor analysis. *J. Internat. Assoc. of Math. Geol.* 3: 61-67.
- Kosugi, M., 1987. Limiting factors on the distribution of benthic diatoms in coastal regions—salinity and substratum. *Diatom* 3: 21-31.
- . 1988. Classification of living diatom assemblages as the indicator of environments, and its application to reconstruction of paleoenvironments. *The Quaternary Research* 27(1): 1-20.
- Laws, R.A., 1988. Diatoms (Bacillariophyceae) from surface sediments in the San Francisco Bay estuary. *Proc. Calif. Acad. Sci.* 45: 133-254.
- Macdonald, K.B., 1977a. Coastal salt marsh. P. 263-294 in M. G. Barbour and J. Major (eds.), *Terrestrial Vegetation of California*. John Wiley and Sons, New York.
- . 1977b. Plant and animal communities of Pacific North American salt marshes. P. 167-191 in V. J. Chapman (eds.), *Wet Coastal Ecosystems*. Elsevier.
- Macdonald, K.B., and M.G. Barbour, 1977. Beach and salt marsh vegetation of the North American Pacific Coast. P. 175-233 in R. J. Reimold and W. H. Queen (eds.), *Ecology of Halophytes*. Academic Press, New York.
- Main, S.P., and C.D. McIntire, 1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon (U.S.A.). *Bot. Mar.* XVII: 88-99.
- Major, S., 1989. An assessment of water quality in Willapa Bay, Washington for EPA's Near Coastal Waters Initiative. Institute for Marine Studies, Univ. Wash.
- McIntire, C.D., 1978. The distribution of estuarine diatoms along environmental gradients: A canonical correlation. *Estuar. Coast. Mar. Sci.* 6: 447-457.
- McIntire, C.D., and W.W. Moore, 1977. Marine littoral diatoms: ecological considerations. P. 333-371 in D. Werner (eds.), *Biology of Diatoms*. University of California Press, Berkeley.
- McIntire, C.D., and W.S. Overton, 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecol.* 52(5): 758-777.
- Moore, W.W., and C.D. McIntire, 1977. Spatial and seasonal distribution of littoral diatoms in Yaquina Estuary, Oregon (USA). *Bot. Mar.* 20: 99-109.
- Nelson, A.R., 1992. Holocene tidal-marsh stratigraphy in south-central Oregon—Evidence for localized sudden submergence in the Cascadia subduction zone. P. 287-301 in C.P. Fletcher and J.F. Wehmiller (eds.), *Quaternary Coasts of the United States: Lacustrine and Marine Systems*. SEPM Spec. Pub. 48.
- Nelson, A.R., and K. Kashima, 1993. Diatom zonation in southern Oregon tidal marshes relative to vascular plants, foraminifera, and sea level. *Journal of Coastal Research* 9(3): 673-697.
- Nelson, A.R., and S.F. Personius, in press. The potential for great earthquakes in Oregon and Washington: An overview of recent coastal geological studies and their bearing on segmentation of Holocene ruptures, central Cascadia subduction zone. In A.M. Rogers, T.J. Walsh, W.J. Kockelman, and G.R. Priest (eds.), *Earthquake Hazards in the Pacific Northwest of the United States*. U.S.G.S. Prof. Paper 1560.
- Palmer, A.J.M., and W.H. Abbott, 1986. Diatoms as indicators of sea-level change. P. 457-487 in O. van de Plassche (eds.), *Sea-Level Research—A Manual for the Collection and Evaluation of Data*. Geo Books, Norwich.
- Plafker, G., 1969. Tectonics of the March 27, 1964 Alaska Earthquake. U.S.G.S. Prof. Paper 543-I.
- Rao, V.N.R., and J. Lewin, 1976. Benthic marine diatom flora of False Bay, San Juan Island, Washington. *Syesis* 9: 173-213.
- Riznyk, R.Z., 1973. Interstitial diatoms from two tidal flats in Yaquina Estuary, Oregon USA. *Bot. Mar.* 16: 113-138.
- Riznyk, R.Z., and H.K. Phinney, 1972. Manometric assessment of interstitial microalgae production in two estuarine sediments. *Oecol.* 10: 193-203.
- Roelofs, A.K., 1984. Distributional patterns and variation of valve diameter of *Paralia sulcata* in surface sediments of southern British Columbia inlets. *Estuar., Coast. Shelf Sci.* 18: 165-176.
- Round, F.E., 1971. Benthic marine diatoms. *Oceanogr. Mar. Biol. Ann. Rev.* 9: 83-139.
- Sayce, K., 1988. Introduced cordgrass, *Spartina alterniflora* Loisel. in saltmarshes and tidelands of Willapa Bay, Washington. FWSI-87058 (TS), U.S. Fish and Wildlife Service.
- Stevenson, R.J., 1984. Procedures for mounting algae in syrup medium. *Trans. Am. Microsc. Soc.* 103(3): 320-321.
- Sullivan, M.J., 1978. Diatom community structure: Taxonomic and statistical analyses of a Mississippi salt marsh. *J. Phycol.* 14: 468-475.
- Taft, C.E., 1978. A mounting medium for fresh-water plankton. *Transactions of the American Microscopical Society* 97: 263-264.
- Torresan, M.E., 1987. Review and comparison of hydrophotometer and pipette method in analysis of fine grained sediment. U.S.G.S. Open-File Rep. 87-514: 1-38.
- Tynni, R., 1986. Observations of diatoms on the coast of Washington. *Geol. Surv. Finland Rep.* 75: 5-25.
- Vos, P.C., and H.D. Wolf, 1988. Methodological aspects of paleo-ecological diatom research in coastal areas of the Netherlands. *Geol. Mijnb.* 67: 31-40.
- . 1993. Diatoms as a tool for reconstructing sedimentary environments in coastal wetlands; methodological aspects. *Hydrobiol.* 269/270: 285-296.
- Whiting, M.C., 1983. Distributional patterns and taxonomic structure of diatom assemblages in Netarts Bay, Oregon. Ph.D. thesis, Corvallis, Oregon, Oregon State University.
- Fos, P.C., and C.D. McIntire, 1985. An investigation of distributional patterns in the diatom flora of Netarts Bay, Oregon, by correspondence analysis. *J. Phycol.* 21: 665-661.
- Williams, R.B., 1965. Unusual motility of tube-dwelling pennate diatoms. *J. Phycology* 1: 145-146.

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Burr J. Betts, Department of Biology, Eastern Oregon State College, 1410 L Avenue, La Grande, Oregon 97850 and

Robert W. Wisseman, Senior Scientist, Aquatic Biology Associates, 3490 NW Deer Run Road, Corvallis, Oregon 97330

Geographic Range and Habitat Characteristics of the Caddisfly *Cryptochia neosa*

Abstract

Cryptochia neosa males were collected in sweepnet samples and from laboratory-reared pupae from six streams widely separated in the Blue Mountains of Oregon and Washington. *C. neosa* seems to be the only species of *Cryptochia* in the Blue Mountains and its range may extend further westward and eastward. *Cryptochia* larvae were collected or observed in 117 low-order, high-gradient streams containing sediment-free woody debris. Larvae attach primarily to submerged wood and bark during the summer, but they also move into mats of damp, decaying leaves in the fall. Most of the 11 habitat characteristics that differed significantly between streams with and without *Cryptochia* can be related to their effect on the sedimentation of attachment sites. The streams inhabited by *Cryptochia* are receiving increased protection in current forest management plans. We suggest that this species should be downgraded from Category 2 to Category 3C of the Federal Rare and Endangered Species List.

Introduction

Cryptochia is a small genus in the Family Limnephilidae (Order Trichoptera). There are seven species confined to montane streams of western North America. *C. pilosa* is widely distributed in the maritime areas of the Pacific Northwest (Wisseman and Anderson 1987), and *C. furcata* has been reported from the interior mountains of Washington, Montana, and British Columbia (Denning 1964). There are very few records for the other five species, which include *C. neosa* from north-eastern Oregon and southeastern Washington and four species known only from California (Denning 1975).

As with many caddisflies, species of *Cryptochia* are differentiated on the basis of male genitalia (see Denning 1975 for a key). Females and larvae of the genus cannot, as yet, be separated to the species level. However, the distinctive larva and its case provide easy identification of the genus. There is a dense fringe of long hairs on the anterior edge of the larval pronotum and there are two curved bands of dense scale hairs appearing to form a crown on the flattened head (Wiggins 1977). The case is tapered lengthwise, is rectangular in cross-section, and is made of transversely arranged bits of wood and bark.

The only published record of *C. neosa* is the holotype male collected June 21, 1952 at 1550 m on Lunch Creek near Prairie City, Grant Co.,

OR (Denning 1954). Unpublished records of *C. neosa* include one male from Whiskey Creek south of La Grande, Oregon (Stamford Smith, Cent. Wash. Univ., pers. comm.) and several males collected in 1974-77 from Goose Creek in the Wallowa Range of the Blue Mountains incidental to a research project conducted by the U. S. Forest Service's Pacific Southwest Forest and Range Experiment Station (Patrick J. Shea, pers. comm.; Butcher 1979). Denning's holotype male is deposited at the California Academy of Sciences. The Whiskey Creek specimen, identified by Stamford Smith at Central Washington University, is deposited in the entomology collection there. The Goose Creek specimens were also identified by Stamford Smith, but their fate and the number of males and females collected are unknown (P. Shea, pers. comm., S. Smith, pers. comm.).

The lack of knowledge about *C. neosa* and its potential rarity led to its classification in 1984 as a Category 2 candidate invertebrate for the Federal Rare and Endangered Species List (Federal Register 1984). A Category 2 species is one for which current information indicates that listing it as threatened or endangered might be appropriate, but for which conclusive data on its biological vulnerability are insufficient to support such a listing (Federal Register 1984). The purpose of this study was to determine the status of this species, including its current geographic range and habitat characteristics.

Methods and Results

Geographic Range

Adults were field-collected and laboratory-reared from streams in several areas of the Blue Mountains. From mid-June to mid-August, 1990 and 1991 we used a muslin butterfly net to sweep streamside vegetation, logs, and moist undercut banks. In May and June, 1992 we collected pupae for rearing. Some pupae, attached to pieces of wood, were placed in screen wire cages that were partially submerged in Tie Creek near La Grande such that the pupae were near, but above water level. Other pupae were placed on moist filter paper in covered Petri dishes and held in a dark environmental chamber at 20°C. Not all pupae eclosed, but some dead pupae were identifiable.

We collected five adult and two pupal male *Cryptochia neosa* and two adult and one pupal female *Cryptochia* from sweepnet samples, captivity-reared pupae, and dead pupae. All specimens have been deposited in the Systematic Entomology Laboratory Collection at Oregon State University. The males were collected from six streams, bringing to nine the number of streams from which this species has been positively identified (Fig. 1). These nine streams are widespread in the Blue Mountains and no other species of *Cryptochia* has been reported from this area. We conclude that *C. neosa* is the only species of *Cryptochia* present in the Blue Mountains, and we assume that all the larvae we found in the Blue Mountains are this species. Because of this assumption, we henceforth use "*Cryptochia*" to represent "*Cryptochia* probably *neosa*" and we use "*Cryptochia* sp" to refer to the genus as a whole.

Cryptochia larvae were more easily found than were adults. Larvae were simply picked from or observed on wood and bark in small streams. We selected most streams on the basis of their accessibility and size. Initial collecting revealed that large, fast streams did not contain *Cryptochia*. Initial collecting also was concentrated in the Wallowa-Whitman National Forest, and we visited fewer streams in outlying areas as we expanded the search for the geographic range limits. Data on locations of *Cryptochia* larvae were also provided by U. S. Forest Service workers in the Umatilla and Malheur National Forests.

We found *Cryptochia* larvae in 117 streams throughout the Blue Mountains (Fig. 1). Because of their wide distribution, no attempt was made to

locate all streams in which they were present. Many of these larvae have also been deposited in the Systematic Entomology Laboratory Collection at Oregon State University; site locations for all specimens collected in this study are available from the first author.

Although the Blue Mountains are isolated from other mountain ranges to the north and south, they are not far from the Ochoco Mountains to the west or from several ranges in Idaho east of Hell's Canyon National Recreation Area. We collected *Cryptochia* larvae in both areas (Fig. 1). Although we suspect these Ochoco and Idaho individuals are *C. neosa*, they might also be *C. pilosa* and/or *C. furcata*. *C. pilosa* has been recorded from the east slopes of the Cascade Mountains (Anderson 1976) about 60 km west of the Ochocos and the Deschutes River system lies between and drains both mountain areas. References to Idaho specimens of *C. pilosa* date back to Ross (1950), but we could not locate the actual record(s) to which he referred. There is an unpublished record of a *C. pilosa* collected in 1974 near Priest River (O. S. Flint, Smithsonian Inst., Washington, D.C., pers. comm.), but this location is in the panhandle area of Idaho well north of our collection sites. *C. furcata* has not been reported south of Washington and Montana (Denning 1964). We have not attempted to capture the adult males necessary to determine the areas of sympatry, parapatry, or possible gap between the ranges of *C. neosa*, *C. pilosa*, and *C. furcata*.

Habitat Characteristics

We characterized the substrates to which larvae cling during the summer by carefully searching for larvae in five streams during July and August, 1992. Substrates were classified as to type, texture, and size. In addition we recorded the location of the larvae on the substrate and the location of the larvae in relation to water line. Lastly, we recorded whether the substrate was located in a riffle, glide, pool, or a debris jam at a pool outlet.

Since *C. pilosa* larvae are known to move into damp leaves during the fall (Wissemann and Anderson 1987), we collected leaves in November, 1993 from three streams known to contain *Cryptochia* larvae. We restricted our collection along the bank to damp leaves, which were usually within 1 m of the water edge and less than 30 cm above the water line. We also collected leaves from the

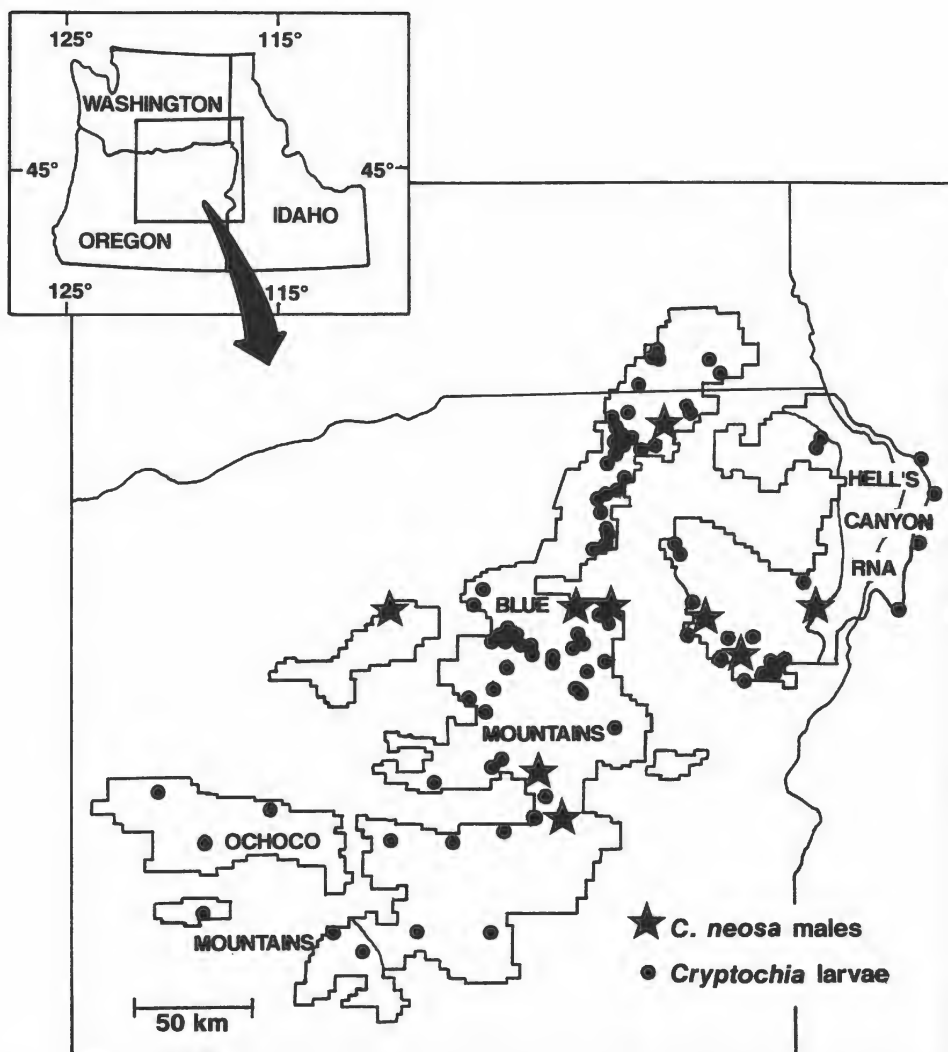


Figure 1. Capture sites for *Cryptochia* larvae and *C. neosa* males in eastern Oregon, southeastern Washington, and western Idaho.

water surface and from behind rocks and debris jams below the water line.

We found *Cryptochia* larvae clinging only to pieces of wood and bark during the summer, although we also found them among the damp, decaying leaves both above and below water line in November. *Cryptochia* larvae found in debris jams at pool outlets during the summer were always clinging to small pieces of wood. In the five

streams searched to characterize substrate types, we found larvae using 212 (90.6%) pieces of wood and 22 (9.4%) pieces of bark. The pieces of wood ranged from small twigs to long limbs. Many streams also contained logs too large to turn over; it is possible that these also provided appropriate sites for larval attachment. The pieces of bark used by *Cryptochia* were mostly large and heavy. Most (210; 89.7%) of the substrate pieces had rough

texture and the wood was partly decayed. The other 24 (10.3%) pieces were smooth.

The location of the larvae on the attachment substrate was determined for 198 larvae. Most (187; 94.4%) were in a position (bottom, downstream side, end crevice) somewhat protected from the current while 11 (5.6%) were on the top or upstream side of the substrate in the direct current. Unlike *C. pilosa* larvae which Wisseman and Anderson (1987) nearly always found in damp organic matter above the water line, we only found one of the 234 larvae above water level during the summer. However, several of the larvae found by Umatilla National Forest workers were reportedly above water line. Finally, we found larvae only in riffle areas (62; 59.0%) and in the debris jams (43; 41.0%) at pool outlets. In both areas water velocity was greater than in pools and glides.

We selected 33 sites for comparing 21 habitat characteristics between streams with and without *Cryptochia*. All eight streams in which extensive searching failed to produce any *Cryptochia* were compared to 25 randomly chosen sites containing *Cryptochia*. At each site we sampled a 100 m section divided into ten equal segments. In each segment we: 1) measured the percent of riffle, pool, and glide and recorded the maximum depth, percent embeddedness, and dominant bottom substrate in each of these flow types; 2) estimated average stream width; 3) measured gradient with a clinometer; 4) counted pieces of wood and bark; 5) measured total canopy cover at mid-segment with a densiometer; 6) estimated percent bank stability on the basis of the amount likely to contribute to sedimentation during spring run-off; and 7) estimated the percent of the bank providing sites where adults might hide during the daytime including cover from trees, shrubs, herbaceous vegetation, undercut bank, and logs.

Bottom substrate differed between streams with and without *Cryptochia* only in riffle areas (riffle: $p=0.007$; pool: $p=0.82$; glide: $p=0.71$; Fisher exact probability test, Siegel 1956). Gravel or larger substrates predominated in the riffles in 24 of the 25 streams containing *Cryptochia*, but sand and silt substrates were present in the riffles in four of the eight streams lacking *Cryptochia*. Streams containing *Cryptochia* larvae also had significantly less substrate embeddedness in all three flow types (riffle, pool, glide) than streams without *Cryptochia* (Table 1).

Streams with *Cryptochia* had significantly more riffle, less glide, shallower glide, steeper gradient, greater total bank stability, more canopy cover, and greater percent tree cover than did streams lacking *Cryptochia* (Table 1). Wood and bark, the predominant summer attachment substrates for *Cryptochia* larvae, also were significantly more common in streams containing *Cryptochia* (Table 1).

Discussion

Cryptochia larvae were widespread in the Blue Mountains. It was typical to find at least one individual within 10 min in any low-order, high-gradient stream containing sediment-free woody debris or bark. However, extensive searching in large streams or in low-gradient streams rarely produced any individuals. We believe this distribution of *Cryptochia* can be related to the availability of appropriate habitat and food.

Cryptochia sp. larvae are primarily grazers (Wiggins and Mackay 1978), but may be partially shredders (Pereira *et al.* 1982). Larval gut contents include fungal hyphae and spores, algae, vascular plant tissue including leaf and wood cells, and other fine particulate organic matter (Wiggins 1977, Pereira *et al.* 1982, Wisseman and Anderson 1987).

Low gradient streams are characterized by siltation which inhibits the growth of fungi and algae and excludes many grazing invertebrates (Dudley and Anderson 1982) including, apparently, *Cryptochia*. Most of the habitat characteristics that differed significantly between streams with and without *Cryptochia* could be related to their effect on the siltation of the woody debris and bark to which *Cryptochia* larvae cling. More riffle and steeper gradients keep sediment moving in streams containing *Cryptochia*, while more glide and deeper glide would allow sediment to settle in streams without *Cryptochia*. These differences, along with lower bank stability, would contribute to the greater substrate embeddedness throughout streams lacking *Cryptochia*.

The greater total canopy cover and percent tree cover in streams with *Cryptochia* may contribute directly to the presence of *Cryptochia* by providing locations for adults to hide. Alternatively, tree and canopy cover may be inversely correlated with such human disturbances as logging and road building that can increase siltation and embeddedness and thus reduce the likelihood of *Cryptochia*

TABLE 1. Comparison of 18 habitat characteristics between streams containing *Cryptochia* larvae and streams where *Cryptochia* larvae were not found.

Habitat characteristic	Streams with <i>Cryptochia</i> larvae			Streams without <i>Cryptochia</i> larvae			P ^a
	N	Mean $\pm$ SD	Range	N	Mean $\pm$ SD	Range	
riffle length/100 m (%)	25	88.4 $\pm$ 10.3	59.5 – 100.0	8	73.7 $\pm$ 26.3	15.0 – 96.0	0.049
pool length/100 m (%)	25	5.7 $\pm$ 5.0	0.0 – 17.5	8	7.2 $\pm$ 8.8	0.0 – 25.0	NS
glide length/100 m (%)	25	5.8 $\pm$ 8.8	0.0 – 39.0	8	19.1 $\pm$ 21.7	4.0 – 70.5	0.007
max riffle depth (cm)	25	14.0 $\pm$ 5.0	7.0 – 29.0	8	15.0 $\pm$ 8.0	9.0 – 34.0	NS
max pool depth (cm)	21	22.0 $\pm$ 6.0	12.0 – 38.0	7	25.0 $\pm$ 18.0	9.0 – 63.0	NS
max glide depth (cm)	14	15.0 $\pm$ 6.0	7.0 – 26.0	8	21.0 $\pm$ 9.0	10.0 – 40.0	0.022
riffle embeddedness (%)	25	4.8 $\pm$ 2.7	0.0 – 11.0	8	35.7 $\pm$ 24.7	16.5 – 83.0	<0.001
pool embeddedness (%)	21	36.3 $\pm$ 25.8	2.0 – 85.0	7	83.0 $\pm$ 10.7	65.8 – 100.0	<0.001
glide embeddedness (%)	14	38.3 $\pm$ 30.0	5.0 – 82.5	8	76.6 $\pm$ 15.4	55.0 – 100.0	0.009
stream width (m)	15	1.3 $\pm$ 0.5	0.5 – 2.8	8	1.3 $\pm$ 0.5	0.8 – 2.0	NS
gradient (%)	25	11.7 $\pm$ 8.1	3.8 – 35.8	8	4.0 $\pm$ 1.6	1.4 – 6.3	<0.001
wood and bark (#/100 m)	25	79.0 $\pm$ 34.0	26.0 – 133.0	8	38.0 $\pm$ 17.0	10.0 – 65.0	0.003
shade cover (%)	25	69.6 $\pm$ 11.8	31.5 – 86.4	8	36.5 $\pm$ 25.3	0.4 – 65.2	<0.001
bank stability (%)	25	90.3 $\pm$ 5.8	74.5 – 99.0	8	81.6 $\pm$ 13.6	57.5 – 97.5	0.048
tree bank cover (%)	25	24.0 $\pm$ 11.0	2.0 – 48.0	8	7.5 $\pm$ 6.4	0.0 – 18.0	<0.001
shrub bank cover (%)	25	37.8 $\pm$ 27.3	3.0 – 87.0	8	22.4 $\pm$ 21.0	0.0 – 47.0	NS
herbaceous bank cover (%)	25	63.9 $\pm$ 18.5	9.0 – 89.0	8	77.1 $\pm$ 19.8	51.0 – 100.0	NS
cutbank, log bank cover (%)	25	22.3 $\pm$ 21.5	2.0 – 99.0	8	13.3 $\pm$ 5.7	5.0 – 20.0	NS

^aMann-Whitney U-test; one-tailed.

being present. Perhaps lower tree and canopy cover in streams without *Cryptochia* may be only incidental to these streams often meandering through open meadows.

Wood provides the major input of organic matter into the headwaters of streams in the coniferous forests of western North America (Dudley and Anderson 1982). The wood standing crop decreases as stream order increases and streams acquire the power to flush out most debris annually (Anderson *et al.* 1978, Dudley and Anderson 1982). What remains in large streams is subject to abrasion, which removes the softer surface layers of the wood that could otherwise be inhabited by various organisms (Dudley and Anderson 1982). *Cryptochia* larvae were uncommon on smooth wood, and the lack of *Cryptochia* in larger streams is most likely related to this paucity of soft, decomposing wood colonized by fungi and algae. The turbulent water in large streams may also be unsuitable for *Cryptochia* larvae, which usually assume a position out of direct current even in smaller streams.

If we are correct in concluding that *C. neosa* is the only species of *Cryptochia* present in the Blue

Mountains, then it is widely distributed. Most of the small order streams that it inhabits are located on national forest land. Concerns about the effects of logging, grazing, and road-building on these streams and their fisheries has led to increased protection in current Forest Service management plans. Thus, we believe that the status of *C. neosa* should be changed from Category 2 to Category 3C. The latter category is for taxa “proven to be more abundant or widespread than was previously believed and/or those that are not subject to any identifiable threat” (Federal Register 1984).

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Literature Cited

- Anderson, N. H. 1976. The distribution and biology of the Oregon Trichoptera. Ore. Agric. Exp. Sta. Tech. Bull. 134:1-152.
- Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. Amer. Midland Nat. 100:64-82.
- Butcher, M. 1979. Drought effects on stream insect populations. M.S. Thesis, Central Washington Univ., Ellensburg, Washington.
- Denning, D. G. 1954. New species of western Trichoptera. J. Kansas Entomol. Soc. 27:57-64.
- . 1964. Descriptions of five new Trichoptera. Pan-Pacific Entomologist 40:241-245.
- . 1975. New species of Trichoptera from western North America. Pan-Pacific Entomologist 51:318-326.
- Dudley, T. and N. H. Anderson. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. Melanderia 39:1-21.
- Federal Register. 1984. Part III, Department of the Interior, Fish and Wildlife Service. 50 CFR Part 17: Endangered and threatened wildlife and plants; Review of invertebrate wildlife for listing as endangered or threatened species. Federal Register 49 (100):21663-21675.
- Pereira, C. R. D., N. H. Anderson, and T. Dudley. 1982. Gut content analysis of aquatic insects from wood substrates. Melanderia 39:23-33.
- Ross, H. H. 1950. Synoptic notes on some nearctic limnephilid caddisflies. Amer. Midland Nat. 43:410-429.
- Siegel, A. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.
- Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. of Toronto Press, Toronto, Canada.
- Wiggins, G. B. and R. J. Mackay. 1978. Some relationships between systematics and trophic ecology in Nearctic aquatic insects with special reference to Trichoptera. Ecology 59:1211-1220.
- Wisseman, R. W. and N. H. Anderson. 1987. The life history of *Cryptochia pilosa* (Trichoptera: Limnephilidae) in an Oregon Coast Range watershed. Pp 243-246 in M. Bournaud and H. Tachet (eds.). Proc. Fifth Int. Symp. on Trichoptera. Junk Publ., Dordrecht, The Netherlands.

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and

Charles R. Knowles, Idaho Geological Survey, Moscow, Idaho 83843

Subsurface Evidence for a Rapid Formation of the Clarkia Miocene Lake in Northern Idaho

Abstract

A recent drilling program across the St. Maries River valley near the town of Clarkia in northern Idaho coupled with geophysical surveys and geochemical studies provides new information on the geologic history of the area and the origin of the Miocene lake deposits near Clarkia. The three drill cores reached the same basement rock at different elevations, and recorded an abrupt lithofacies shift from coarse-grained alluvial sediments at the lower part to fine-grained lacustrine sediments in up-section. Lake sediments were correlated across the lacustrine deposits in the study area by both physically tracing and geochemically comparing distinctive volcanic marker beds. Geophysical data derived from magnetic and seismic surveys were consistent with the borehole data and indicate that eroded Precambrian metamorphic rocks of the Wallace Formation (Belt Supergroup) served as an irregular basin floor above which relatively coarse-grained Cenozoic alluvium were initially deposited in at least two parallel, north-south trending channels which were separated by a prominent divide. The subsurface data reveal a rapid formation of the Miocene lake environment above the channel deposits. The new subsurface data gathered in this investigation support the previous findings based on limited surface geologic data and conclude that the Miocene lake was rapidly created by a Columbia River basalt flow damming the preexisting proto-St. Maries River drainage.

Introduction

When geologists first mapped the Pacific Northwest area, they recognized the close relationship between the Columbia River basalts and interbedded lacustrine (lake) sediments near the eastern border of the Columbia Plateau. Some geologists speculated that lakes formed when basalt flows dammed ancient river valleys (Kirkham 1926; Anderson 1927, 1928). Deposits from one of these ancient lakes near Clarkia (the Clarkia Miocene lake) (47°00'N, 116°15'W) in Shoshone County, northern Idaho is renowned for its extraordinarily preserved fossil materials. These materials yielded intact cellular tissues retaining paleobiomolecules and rare records of Tertiary plant fossil DNA (Smiley *et al.* 1975; Niklas and Brown 1981; Giannasi and Niklas 1981; Smiley 1985; Niklas *et al.* 1985; Rieseberg and Soltis 1987; Giannasi 1990; Golenberg *et al.* 1990; Golenberg 1991; Soltis *et al.* 1992; Logan *et al.* 1993). The fine preservation of the fossil materials is strongly controlled by paleolimnologic factors which are related to the origin and development of the ancient lake. Smiley *et al.* (1975) suggested that the Clarkia Miocene lake originated from a Columbia River basalt flow damming the preexisting proto-St. Maries River valley. Smiley and Rember (1981, 1985) further con-

cluded that the paleodrainage of the proto-St. Maries River was similar to the present-day St. Maries River based on geomorphologic evidence, structural trend, and relative tectonic stability of the region since the Neogene. However, because previous geologic and paleoecologic investigations of the lake history were primarily inferred from outcrop data (Smiley and Rember 1979, 1981, 1985; Smiley 1989; Rember 1991), potentially valuable insight into the origin and early history of the lake has remained speculative. The study described in this paper addresses this problem by augmenting existing surface geologic and geomorphologic understanding using subsurface borehole and geophysical data. The new subsurface data has permitted us to reconstruct the thickness of sediments, to determine the shape of the bedrock surface, and assess the overall depositional history. Data were collected from three drill cores, as well as from magnetic and seismic surveys during the summer of 1991.

Methods

Magnetic and seismic reflection surveys were carried out along a 1143 m line in an east-west direction across the river valley. The line began at the main fossil site (University of Idaho Mines Museum P-33) (Figure 1), where the depth to basement was known from stratigraphic correlations with nearby drill core Cl #1. The line extended eastward across the valley through the sites of drill core Cl #2 and

¹Present address: Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202

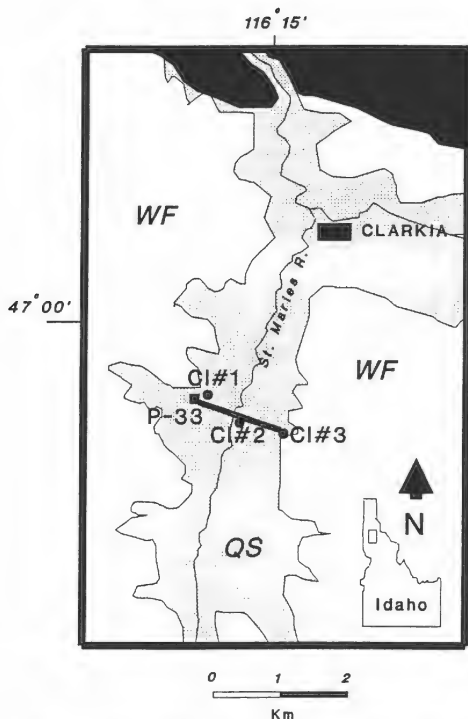


Figure 1. Location map showing geophysical transect line (from P-33 to CI#3), drill sites (CI#1, CI#2, and CI#3; circles), and the main fossil site (P-33, square) in the St. Maries River valley near Clarkia. WF=Precambrian Wallace Formation (gneiss and schist), CRB=Tertiary Columbia River Basalt Group (basalt), QS=Quaternary sediments (gravels and soil), which largely are underlain by Miocene lake sediments (laminated siltstone). The St. Maries River flows toward the north.

CI#3, both of which reached basement. These known depths to bedrock permitted a well-constrained interpretation of the seismic results. Proton precession magnetometers were employed by two independent survey groups to measure the total field strength of the geomagnetic field to a sensitivity of one gamma at 15.2 m intervals along the line. A trans-basin seismic reflection profile was completed along the same line. A ES1210F 12-channel seismograph was used to make paper recordings of the seismic reflections in the field. High frequency (100 Hz) geophones, closely spaced at 3 m intervals, were placed along the survey line from 79 to 107 m west of the shot. The energy source was a steel plate and sledge hammer. Hammer blows were continued until a strong reflected signal appeared on the seismograph records. Reflec-

tions on the original records were initially identified and tabulated by hand, and then processed by computer.

In order to perform static and dynamic corrections for the reflection times, the following data were tabulated: geophone locations, shot locations, delay times, first-break times, and raw reflection times (Yang 1993). Because the seismic line was on gently inclined topography, no elevation corrections were applied. However, it is important to note that, because elevation corrections were not applied, the resulting seismic section is a depth profile, tied to the ground surface rather than to a particular elevation datum. The actual surface elevations (above sea level) are 871 m at site P-33 on the west side of the valley, 865 m in the central area including hole CI#2, and 875 m at hole CI#3 on the east side of the valley. Most records showed a reflection velocity from 1220 to 2135 m/sec, with an average of 1678 m/sec. This was interpreted to be the seismic velocity of saturated sediments in the valley. We used this constant velocity for the dynamic correction for migration and to convert reflection times to depth for the final results.

An Acker drill vehicle was used for the drilling operation, and standard drilling procedures were followed during the project. The present elevation of each drill site was determined using an altimeter (accurate to 0.5 m). A 1.5 m interval tube was used to obtain 6.4 cm diameter cores which were logged at the drill site immediately after they were brought to the surface. Lithology, color, mineral composition, fossil content, and sedimentary structure were investigated when the cores were still wet. The drill cores were reexamined under a reflected light microscope, and lithologic subunits were determined in the laboratory.

In order to preform the stratigraphic correlation of the drill cores, we selected volcanic ash samples from the lowermost ash layer of each drill core and from the P-33 outcrop (Figure 1 and Figure 3) for electron microprobe analysis. The samples were prepared on glass slides following the methods of Smith *et al.* (1975). Ten or more shards were examined for each slide, and at least five particles were analyzed in various locations within the shard. Energy dispersive spectroscopic (EDX) methods were used to determine all elements present in amounts greater than approximately 0.01%, but we report only those for Fe, Ca, and K since these three elements were previously found useful for characterizing the glass component of similar volcanic ash (Smith *et al.* 1975).

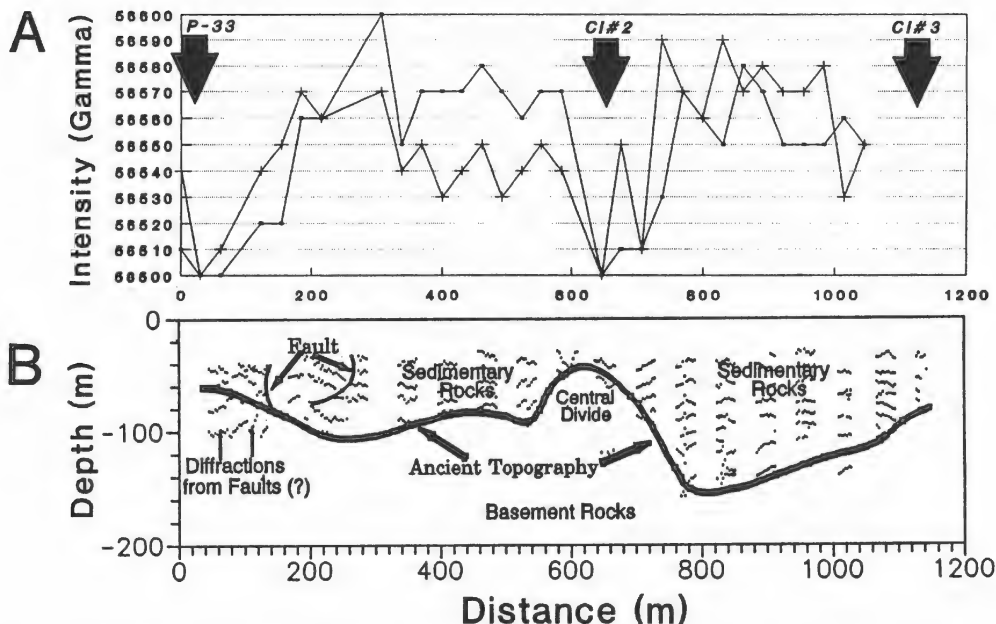


Figure 2. Geophysical survey across the St. Maries River valley. Distances are from the west end of the line. 2A. Variation of geomagnetic intensity showing two negative anomalies detected by two independent survey groups (marked crosses and dots); 2B. seismic reflection profile showing pre-Tertiary topography, Tertiary sedimentary sequences, post-deposition faulting, and possible diffractions related to the faults. The wiggling lines represent apparent seismic reflectors in their true subsurface positions.

Results and Interpretations

The results of the magnetic survey are plotted in Figure 2A. Large negative magnetic anomalies of about 50 gammas were detected at distances of 50 and 650 m from the west end of the line. We believe that the negative anomalies indicate locally high bedrock topography. Although no actual magnetic susceptibility measurements were made as part of the study, our interpretation is consistent with the composition of the bedrock and valley fill as revealed in the drill cores. The bedrock is metasedimentary gneiss, whereas the overlying valley fill contains coarse sand and gravels derived in part from the garnet schists of the surrounding mountains. Magnetite, known to be associated with the garnets in the area, is the most likely source of the higher magnetization of the valley fill compared to the bedrock.

The migrated seismic depth section with superimposed interpretations is shown in Figure 2B. The data points forming wiggling lines represent migrated subsurface reflecting points in their correct positions relative to the ground surface. On the seismic section, the bedrock surface is revealed both

by the dip of the reflections and by the absence of deep reflections from the underlying crystalline rock. Our interpretation of the combined magnetic and seismic data is as follows: (1) The geology along the E-W transect line appears to consist of at least two sedimentary depocenters separated by a prominent central divide in the middle part of the survey line, near 625 m on Figure 2B. (2) The central divide is surrounded by largely undisturbed horizontally-layered sediments. Relatively high ridges of the basement also occur near both sides of the valley. (3) To the east of the central divide, the deep ancestral valley appears to be centered near 800 m on Figure 2B, where flat reflections from depths of at least 150 m are apparent. (4) To the west of the central divide, reflectors are apparent to depths approaching 100 m in a separate ancestral valley near 250 m on Figure 2B.

Several of the seismic events apparent on Figure 2B are apparently not true reflectors. These include the west-dipping seismic signals deep below P-33 and the distorted seismic events above the central divide. The seismic signals from below the inferred basement surface near P-33 on Figure 2B are interpreted to be diffraction patterns

TABLE 1. Electron microprobe analysis of Fe-Ca-K content in volcanic ash samples from the Clarkia deposits

Sample#	Location	Weight % of			Proportion of Fe:Ca:K
		Fe	Ca	K	
C1	Cl#1 Lowest ash	0.86	0.38	6.39	11:5:84
C2	Cl#2 Lowest ash	0.93	0.34	5.06	15:5:80
C3	Cl#3 lowest ash	0.93	0.34	5.15	14:5:80
S1	P-33 Top ash*	1.48	1.07	2.99	27:19:54
S2	P-33 Middle ash**	3.89	1.00	4.23	43:11:46
S3	P-33 Lower ash***	2.72	1.00	2.99	41:15:45

Ash layers on P-33 outcrop correspond to *Unit 5b, **Unit 4, and ***Unit 2c of Smiley and Rember (1985)

from faults in the overlying alluvial sediments. Although the presence of these diffraction patterns suggests that post-sedimentation faulting has occurred, the sense or amount of offset on the intervening faults is unclear. The distorted seismic events above the shallow central divide are probably matching the volcanic ash layers with the near by P-33 type section documented by Smiley and Rember (1985). The three drill cores are correlated by a unique pyroclastic marker bed (pumice lapilli) that was deposited across the St. Maries River valley; the correlation is confirmed by electron microprobe analysis of selected volcanic ash samples taken from the lowermost ash layers (Table 1). A close match of gross lithologies and sedimentary structures among the three drill cores also support such a correlation. The three ash samples (C1, C2, and C3), taken from the lowest ash layers of drill cores Cl#1, Cl#2, and Cl#3, are very similar in chemical composition and are clustered well in the Fe-Ca-K ternary diagram (Figure 4). On the other hand, the ash samples obtained from the P-33 outcrop (S1, S2, and S3) are apparently correlative to the upper ash layers of Cl#1 nearby. These samples have different chemical signatures from the lower ash layer in the drill cores. Although

the corresponding pyroclastic layers were not encountered at the same elevation in different drill cores (Figure 3), the fact that the lacustrine beddings dip gently east (less than 4 degrees), post-depositional faulting, and irregular topography of the bottom of the ancient lake may have disturbed the original horizontality of these lake sequences. The lacustrine deposits were incomplete in the study area. A soil horizon marking surface erosion appears in drill cores and at the P-33.

The three drill cores encountered the same basement rock lithology at different depths, supporting the geophysical interpretation that the valley sediments did not fill a simple V-shaped valley. From drilling results, the depth to basement is 60 m at P-33, 40 m at Cl#2, and 83 m at Cl#3. The interpreted basement surface on the seismic section very closely corresponds to these depths (Figure 2B). Above the basement, the cores can be divided into two major phases: a light-colored and coarse-grained fluvial phase at the lower part and a dark-colored and fine-grained lacustrine phase (topped by a thin soil layer) in the upper part. The fluvial phase is dominated by coarse siltstone, fine sandstone, interbeddings of unconsolidated gravels, and peat layers. Black-colored wood (logs ?) are commonly encountered in units of the lower part. The composition of the unconsolidated gravels in the middle and upper parts of the fluvial phase consists of quartzite, quartz monzonite, granite, gneiss, and garnet schist. A layer of clast-supported conglomerate containing mainly garnet schist and gneiss was encountered only in the bottom of Cl#1. The conglomerate differs from the unconsolidated gravels in both composition and cementation. A rapid lithofacies shift from a fluvial phase to a

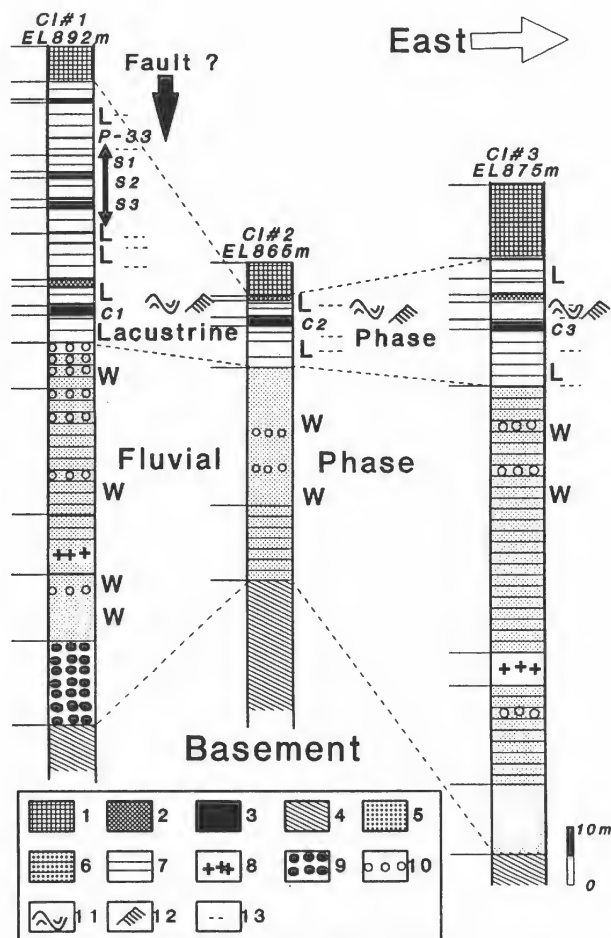


Figure 3. Drill core records (Cl#1, Cl#2, and Cl#3) showing stratigraphic sequence, lithology, sedimentary structure, fossil content, and paleoenvironmental change. The correlation is based on lithology, sedimentary structure, and chemical composition of interbedded pyroclastic rocks. P-33 = type section outcrop (arrow range) documented by Smiley and Rember (1985); EL = drill site elevation. S1, S2, and S3 are ash samples from P-33. C1, C2, and C3 are ash samples from the lowermost ash layer in drill cores. Legends: 1 = soil layer, 2 = pumice layer, 3 = volcanic ash, 4 = gneiss, 5 = sandstone, 6 = sandstone and siltstone, 7 = siltstone, 8 = peat layer, 9 = conglomerate, 10 = gravel, 11 = convolute structures, 12 = cross beddings, 13 = laminations, W = log wood, L = fossil leaves.

lacustrine phase is recorded in all three drill cores. Such a phase change is represented by a sharp contact between the two lithofacies, indicating a geologically-instantaneous event. The lacustrine phase, whose upper part can be readily correlated with the P-33 outcrop, consists of finely graded, dark colored, and commonly laminated siltstones with interbedded light-colored pyroclastic rocks.

A turbidite unit containing convolute structures and cross beddings is also present in the lower part of the lacustrine phase. Abundant fossil plants and rare fish and insect fossils with excellent preservation were found in several intervals of the lacustrine section. The drill core and previously-documented outcrop data (Smiley and Rember, 1985) show that a majority of the lacustrine section represents an

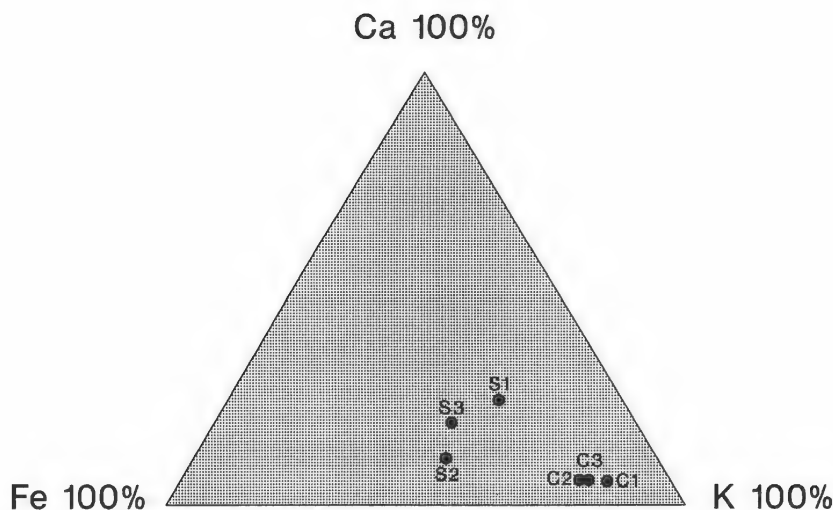


Figure 4. Triangular diagram presenting electron microprobe data for Fe, Ca, and K (sum=100%) from outcrop P-33 (S1, S2, and S3) and from three drill cores (C1, C2, and C3) showing cluster of ash samples from the drill cores. Also see Figure 3 for stratigraphic positions of the samples.

off-shore depositional environment, which was temporally disturbed by volcanic ash falls and turbidite flows, within a deep and water-stratified lake basin.

Discussion

The eruption of Columbia River basalt totally changed the landforms in the Pacific Northwest by filling valleys with lava and causing drainage disruptions. The sedimentary sequences that are associated with the basalt bear critical information needed to understand the Neogene paleogeographic, tectonic, and volcanic development of the region. However, the depositions on and adjacent to the Columbia Plateau have received only preliminary studies (Smith *et al.* 1989). As one of these fluvial-lacustrine sequences, the Clarkia deposits not only provide extraordinary fossil material but also serve as a window to observe the consequences of lake development following the regional volcanic activities. The subsurface data from geophysical surveys and drill cores reveal the geologic development of the sedimentary sequences near Clarkia. The uneven elevations of basement rock, detected by the geophysical surveys and encountered in the drill cores, represent a major unconformity marked by a pre-Miocene topography which contrasts with the present valley configuration. The buried cen-

tral divide trending north to south in the middle of the present St. Maries River valley apparently separated the pre-Miocene paleodrainage system into eastern and western channels. The difference of clast composition in the fluvial phase between the Cl#1 conglomerate (garnet schist clasts) and the Cl#3 gravels (quartzite and quartz monzonite composition) also indicates the separation of stream channels. Garnet schist bedrock is restricted west of the modern St. Maries River valley (Hietanen 1961, 1963, 1984), and quartzite and quartz monzonite are abundant from sources in south and east of the ancient river drainage. When the two separate channels were gradually water-filled to the level of the central divide, organic matter started to accumulate as recorded by the peat layers and dark sandstones and siltstones in the lower parts of Cl#1 and Cl#3.

The major shift of lithofacies from fluvial to lacustrine facies occurred in a relatively short period of time, as indicated by a sharp contrast between the two lithofacies in the three drill cores. The new data of this study indicate that the Clarkia Miocene lake was abruptly created above the ancient river channels. All three drill cores recorded a sharp contact between coarse-grained alluvium and fine-grained lacustrine sediments. Such a manner of lake origin supports the hypothesis of Smiley *et al.* (1975) that the Clarkia Miocene

lake was formed by a natural dam blocking the proto-St. Maries River drainage. Also, the turbidite deposits recorded in the lower part of the lacustrine phase are consistent with relatively steep slopes which are common in a dammed river valley. Based on lithofacies and taphofacies data, previous investigators have suggested that the ancient lake has an oligotrophic water body (Yang, 1993) with a cool and anoxic hypolimnion (Smiley and Rember 1981; Smith and Elder 1985; Bradbury *et al.* 1985; Smiley 1989). The subsurface records reinforce these previous conclusions.

The configuration of the Miocene lake was reconstructed as a large and narrow basin based on the assumption that a lava dam occurred near Mashburn Junction, northwest of Clarkia (Smiley and Rember 1981, 1985; Smiley 1989). However, it is important to emphasize that although the presence of plateau-type basalts downgradient of the proto-St. Maries River valley suggests the possible location and form of the Miocene dam, the present data cannot conclusively reconstruct the specific timing and location of the dam. The source(s) of the basalt flows in Clarkia area has been controversial. Dort (1967) and Bishop (1969) believed that the St. Joe valley and St. Maries valley basalts may have originated from local sources. However, Griggs (1973, 1976) believed that all basalt flows in the Clarkia region belong to the Columbia River Basalt Group. Swanson *et al.*

(1979, 1981) further suggested that basalts in this area belong to either the Priest Rapids Member or the Eckler Mountain Member of the Wanapum Formation on the basis of chemical similarity. Although the radiometric dates of sequence of the Columbia River Basalt Group are now readily available (Reidel and Hooper 1989), the lack of direct contacts between the basalt and P-33 lacustrine sediments makes it difficult to narrow down a precise age for the ancient lake. We plan to directly date the volcanic ash that is interbedded in the P-33 and the lacustrine section of the drill cores. If the chronologic relationship between the lake deposits and the basalt flows can be established, the location and timing of the Miocene dam may be pin-pointed.

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References Cited

- Anderson, A. L. 1927. Some Miocene and Pleistocene drainage changes in northern Idaho. Idaho Bureau of Mines and Geology Pamphlet 18:1-29.
- Anderson, A. L. 1928. A geological reconnaissance in the St. Maries region, Idaho. Idaho Bureau of Mines and Geology Pamphlet 30:1-22.
- Bishop, D. T. 1969. Stratigraphy and distribution of basalt, Benewah County, Idaho. Idaho Bureau of Mines and Geology Pamphlet 140:1-20.
- Bradbury, J. P., K. V. Dieterich, and J. L. Williams. 1985. Diatom flora of the Miocene lakebeds near Clarkia in northern Idaho. In C. J. Smiley (ed.) Late Cenozoic History of the Pacific Northwest. Pacific Division, AAAS, San Francisco. Pp.33-60.
- Dort, W. 1967. Late Cenozoic volcanism, St. Joe River valley, Idaho. Northwest Science 41:141-151.
- Giannasi, D. E., and K. J. Niklas. 1981. Comparative paleo-biochemistry of some fossil and extant Fagaceae. American Journal of Botany 68:762-770.
- Giannasi, D. E. 1990. The Clarkia "fossil" leaves: windows to the past. Northwest Science 64:232-235.
- Golenberg, E. M. 1991. Amplification and analysis of Miocene plant fossil DNA. Philosophical Transactions of Royal Society of London B333:419-427.
- Golenberg, E. M., D. E. Giannasi, M. T. Clegg, C. J. Smiley, M. Durbin, D. Henderson, and G. Zurawski. 1990. Chloroplast DNA sequence from a Miocene *Magnolia* species. Nature 334:656-658.
- Griggs, A. B. 1973. Geologic map of the Spokane quadrangle, Washington, Idaho, and Montana. United States Geological Survey Miscellaneous Geologic Investigations Map I-768, Scale 1:250,000.
- _____. 1976. The Columbia River Basalt Group in the Spokane quadrangle, Washington, Idaho, and Montana. United States Geological Survey Bulletin 1413:1-39.
- Hietanen, A. 1961. Relation between deformation, metamorphism, metasomatism, and intrusion along the north-west border zone of the Idaho batholith, Idaho. United States Geological Survey Professional Paper 424-D:161-164.
- _____. 1963. Metamorphism of the Belt Series in the Elk River-Clarkia area of Idaho. United States Geological Survey Professional Paper 344-C:1-49.

- _____. 1984. Geology along the northwest border zone of the Idaho Batholith, northern Idaho. United States Geological Survey Bulletin 1608:1-17.
- Kirkham, V. R. D. 1926. Ground water for municipal supply at St. Maries, Idaho. Idaho Bureau of Mines and Geology Pamphlet 17:1-10.
- Logan, G. A., J. P. Boon, and G. Eglinton. 1993. Biopolymer preservation in Miocene leaf fossils from the Clarkia site, northern Idaho. Proceedings of the National Academy of Sciences of the USA 90:2246-2250.
- Niklas, K. J., and R. M. Brown. 1981. Ultrastructural and paleobiochemical correlations among fossil leaf tissues from the St. Maries River (Clarkia) area, northern Idaho USA. American Journal of Botany 68:332-341.
- Niklas, K. J., R. M. Brown, and R. Santos. 1985. Ultrastructural states of preservation in Clarkia angiosperm leaf tissues: implications on modes of fossilization. In C. J. Smiley (ed.) Late Cenozoic History of the Pacific Northwest. Pacific Division, AAAS, San Francisco. Pp.143-152.
- Reidel, S. P., and P. R. Hooper. (eds.). 1989. Volcanism and Tectonism in the Columbia River Flood-basalt Province. Geological Society of America Special Paper 239, Colorado.
- Rember, W. C. 1991. Stratigraphy and paleobotany of Miocene lake sediments near Clarkia, Idaho. University of Idaho, Moscow. Ph.D. Dissertation.
- Rieseberg, L., and D. E. Soltis. 1987. Flavonoids of fossil Miocene *Platanus* and its extant relatives. Biochemical Systematics and Ecology 15:109-112.
- Smiley, C. J. (ed.) 1985. Late Cenozoic History of the Pacific Northwest. Pacific Division, AAAS, San Francisco.
- _____. 1989. The Miocene Clarkia fossil area of northern Idaho. In V. E. Chamberlain, R. B. Breckenridge, and B. Bonnicksen (eds.) Guidebook to the Geology of Northern and Western Idaho and Surrounding Area. Idaho Geological Survey Bulletin 28. Pp.35-48.
- Smiley, C. J., J. Gray, and L. M. Huggins. 1975. Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho. Journal of Paleontology 49:833-844.
- Smiley, C. J., and W. C. Rember. 1979. Guidebook and Road Log to the St. Maries River (Clarkia) Fossil Area of Northern Idaho. Idaho Bureau of Mines and Geology, Information circulation, Moscow.
- _____. 1981. Paleocology of the Miocene Clarkia lake (northern Idaho) and its environs. In J. Gray, A. J. Boucot, and W. B. N. Berry (eds.) Communities of the Past, Hutchinson Ross Publishing Company, Stroudsburg, Pennsylvania, Pp.551-190.
- _____. 1985. Physical setting of the Miocene Clarkia fossil beds, northern Idaho. In C. J. Smiley. (ed.) Late Cenozoic History of the Pacific Northwest. Pacific Division, AAAS, San Francisco. Pp.11-32.
- Smith, G. A., B. N. Bjornstad, and K. R. Fecht. 1989. Neogene terrestrial sedimentation on and adjacent to the Columbia Plateau; Washington, Oregon, and Idaho. In S. P. Reidel, and P. R. Hooper (eds.) Volcanism and Tectonism in the Columbia River Flood-basalt Province: Boulder, Colorado, Geological Society of America Special Paper 239, Pp.187-198.
- Smith, G. R., and R. L. Elder. 1985. Environmental interpretation of burial and preservation of Clarkia fishes. In C. J. Smiley (ed.) Late Cenozoic History of the Pacific Northwest. Pacific Division, AAAS, San Francisco. Pp.85-93.
- Smith, H. W., R. Okazaki, and C. R. Knowles. 1975. Electron microprobe analysis as a test of the correlation of west blacktail ash with Mount St. Helens pyroclastic layer T. Northwest Science 49:209-215.
- Soltis, P. S., D. E. Soltis, and C. J. Smiley. 1992. An *rbcl* sequence from a Miocene *Taxodium* (bald cypress): Proceedings of the National Academy of Sciences of the USA 89:449-451.
- Swanson, D. A., T. L. Wright, P. R. Hooper, and R. D. Bentley. 1979. Revisions in stratigraphic nomenclature of the Columbia River Basalt Group. United States Geological Survey Bulletin 1457-G:1-59.
- Swanson, D. A., J. L. Anderson, V. E. Camp, P. R. Hooper, W. H. Taubeneck, and T. L. Wright. 1981. Reconnaissance geologic map of the Columbia River Basalt Group, northern Oregon and western Idaho. United States Geological Survey Open File Report 81-797, Scale 1:250,000.
- Yang, H. 1993. Miocene lake basin analysis and comparative taphonomy: Clarkia (Idaho, U.S.A.) and Shanwang (Shandong, P.R. China). University of Idaho, Moscow. Ph.D. Dissertation.

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The Enterprise Gravel: The Ancestral Wallowa River and Neotectonism in Northeastern Oregon.

Abstract

The Enterprise Gravel includes silt, sand, gravel, diamict, two paleosols, and the Chief Joseph tephra. It includes a well-preserved assemblage of vertebrate fossils in exposures in the Joseph Upland north of Wallowa Lake, northeastern Oregon. Based on fission-track age and magnetic polarity, the Enterprise Gravel is late Pliocene to middle Pleistocene in age. Sedimentologic criteria suggest that exposures of the Enterprise Gravel represent deposits of the ancestral Wallowa River flowing northward across the Joseph Upland. Modern drainage patterns indicate that the region underwent deformation after deposition of the Enterprise Gravel, which caused drainage reversal and realignment of the course of the Wallowa River.

The Enterprise Gravel is unique in that it preserves the previously unknown Chief Joseph tephra, and one of few vertebrate fossil assemblages of late Pliocene to mid-Pleistocene age in the Pacific Northwest. Study of the deformation of the Enterprise Gravel adds to the existing knowledge of the neotectonic history of the region.

Introduction

Location and Previous Work

The study area extending from a moraine complex at Wallowa Lake to the valley of Trout Creek some 15 km north of Enterprise, along the northeast face of the Wallowa Mountains (Figure 1) includes sediments that overlie the Miocene Columbia River Basalt Group. These sediments comprise a sequence of Quaternary fluvial and glaciofluvial sand, silt, and gravel (Crandell, 1967). Newcomb (1969) briefly described the geology and physiography of the region north of Enterprise, which he termed the Joseph Upland.

The bedrock and sediment cover of the region was mapped by Walker (1977, 1979); he included the Enterprise Gravel of this report with the Pliocene McKay gravels, the bulk of which are exposed to the northwest in the Pendleton region (Baldwin, 1986).

Significance of Study

In this study we define and characterize the Enterprise Gravel, and propose mechanisms by which it was deposited. The interpretation of the origin, age, and significance of the Enterprise Gravel involved integration of geomorphology, sedimentology, paleontology, and structural geology, plus various methods of age-determination. This interdisciplinary approach to problem solving resulted in a better understanding of the late Cenozoic geologic history of the Wallowa Lake region.

The Enterprise Gravel

Definition and Type Locality

The Enterprise Gravel is here defined as a sequence of silt, sand, diamict, and gravel exposed between the town of Joseph and the drainage divide between the Grande Ronde and Wallowa Valleys (Figure 1). The name is derived from the town of Enterprise, Oregon, and a type locality (indicated as site 5 on Figure 1) is designated at outcrops along Highway 82 west of Enterprise. The type locality is in the NW 1/4 of sec. 2 and the NE 1/4 of sec. 3, T.2S., R.44E. Between the Chief Joseph Monument and downtown Enterprise are about 0.5 km of outcrops of the Enterprise Gravel on the north side of Highway 82.

Distribution and Topographic Expression

The Enterprise Gravel is exposed in terrace segments north of Joseph and also flanking the valley of Trout Creek north of Enterprise (Figure 1). The best exposures are in a roadcut west of Enterprise and in about a dozen gravel pits scattered across the study area.

The Enterprise Gravel is easily distinguishable on the basis of topographic expression, from the gravel, sand, and silt of the youngest outwash plains and the modern floodplains along Hurricane Creek and the Wallowa River. Figure 2a (section A-A', Figure 1) shows a topographic cross-section from moraines at Wallowa Lake north to Enterprise; Figure 2b (Section B-B', Figure 1) is from Sheep Ridge in the Wallowa Mountains northeastward to Enterprise. The outwash plain is graded from the outlet

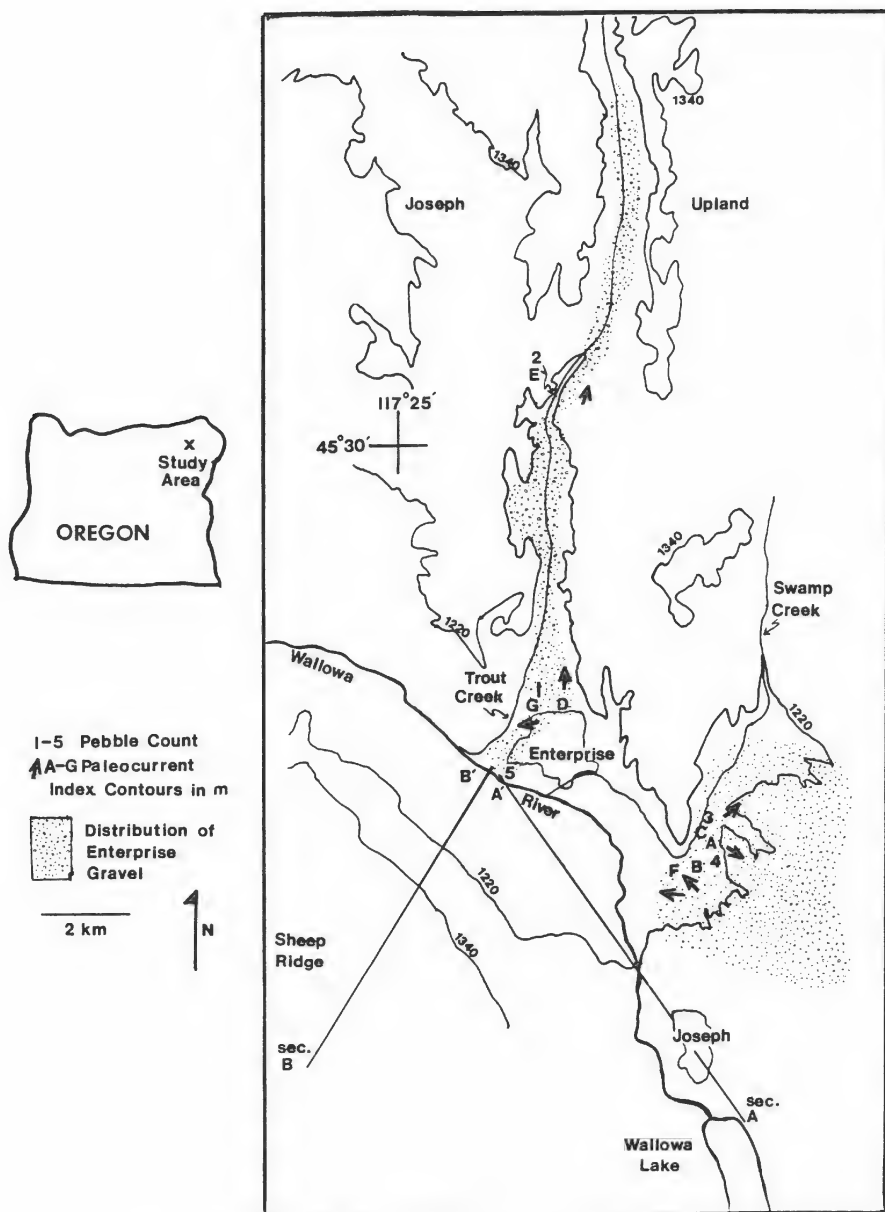


Figure 1. Index map of the Wallowa Lake-Joseph Upland region showing approximate distribution of the Enterprise Gravel (shaded pattern); pebble count locations (1-5); paleocurrent locations (A-G; arrows indicate approximate average paleocurrent for each site); and cross-section lines.

for Wallowa Lake to the modern floodplains of Hurricane Creek and the Wallowa River. Alluvial fans of Alder Slope flanking the study area to the west and southwest are also graded to the modern rivers. Terrace segments and outcrops of the Enterprise Gravel stand topographically above the modern floodplain surfaces and appear to be erosional remnants of a more ancient topographic surface.

Measurements with a surveying altimeter of surface altitude of terraces composed of Enterprise Gravel show that the upper surface of the Enterprise Gravel at the type locality is 30 meters above Hurricane Creek (Figure 2a). Between Joseph and Enterprise the upper surface of the Enterprise Gravel decreases in elevation in a northwesterly direction, consistent with the gradient of the Holocene floodplain and defining the slope of the ancient topographic surface. In the Trout Creek valley the surface of the Enterprise Gravel increases from 1174 meters at the type locality (Loc. 5, Figure 1) to a maximum of 1250 meters at a point 15 km north of Enterprise. The south-sloping gradient is 5.6 m/km.

Sedimentology and Facies

The Enterprise Gravel comprises a sequence of massive to well-stratified silt, sand, diamict, and gravel with complex facies associations. In addition, a tephra horizon is preserved, along with a B-horizon paleosol. At the type locality, the facies used to define the Enterprise Gravel are well-developed. Exposures at other localities are less variable, but can be linked to the type locality based on criteria such as terrace-surface elevation, soils, clast lithology, sedimentary structures, and sedimentary textures. Figure 3 shows idealized facies relationships in a composite stratigraphic column.

Facies Units

Silt Facies: At the type section silt facies generally occur as localized lenses bounded by erosional surfaces. Silts are massive, moderately well-sorted, and poorly indurated. This facies also contains caliche-coated root casts. At other localities, silts occur as rip-up clasts.

Sand Facies: Sand occurs primarily as lenses bounded by erosional lower contacts and either erosional or gradational upper contacts. This

facies displays poor sorting, with significant proportions of silt and fine gravel in most lenses. Planar and trough cross-stratification is common.

Gravel Facies: Gravel is abundant at the type locality and is the dominant textural component of other localities. Nearly all of the gravel is sandy, clast supported, and silt-poor. Lower contacts are erosional and commonly trough shaped; the scale of troughs is about 0.5 meter and they display cross-stratification. Upper contacts are erosional or gradational with sandy intervals.

Diamict Facies: In addition to the silt, sand, and gravel, the Enterprise Gravel includes massive, very poorly sorted diamict exposed at the type and other localities. Diamicts are matrix-supported and contain angular clasts.

Paleosol Facies: A well-developed, purplish, clayey B-horizon paleosol is persistent across the exposed section at the type locality. This unit is present at other outcrops of the Enterprise Gravel as rip-up clasts but has not been recognized in place.

Additionally, the Enterprise Gravel is capped by a well-developed pedocal. This facies is not exposed at the type locality, but is present at the top of most of the remnant terrace segments in the study area. The stage of development of this soil suggests that it is associated with the Enterprise Gravel rather than with the Holocene soil, and that it represents a period of soil development preceding dissection of the ancient surface of the Enterprise Gravel.

Tephra Facies: Associated with the B-horizon soil is a tephra, here named the Chief Joseph tephra (CJt). The CJt is discontinuous at the type locality, and has not been recognized at any other exposure of the Enterprise Gravel. It ranges in thickness from one to about ten centimeters and is preserved as a horizon in the silt facies.

Vertebrate Fossil Facies: Near the top of the type section vertebrate fossils comprise a diverse, well-preserved suite of large and small mammals, including a Perissodactyl (horse), a suid (wild pig), a canid (wolf or coyote), and at least one bird. Fossils have been recovered in other parts of the type locality and at other localities, but these are rare and in poor condition. Spencer and Barnosky (1986) studied some of the taphonomic aspects of the fauna and proposed several explanations for the excellent preservation.

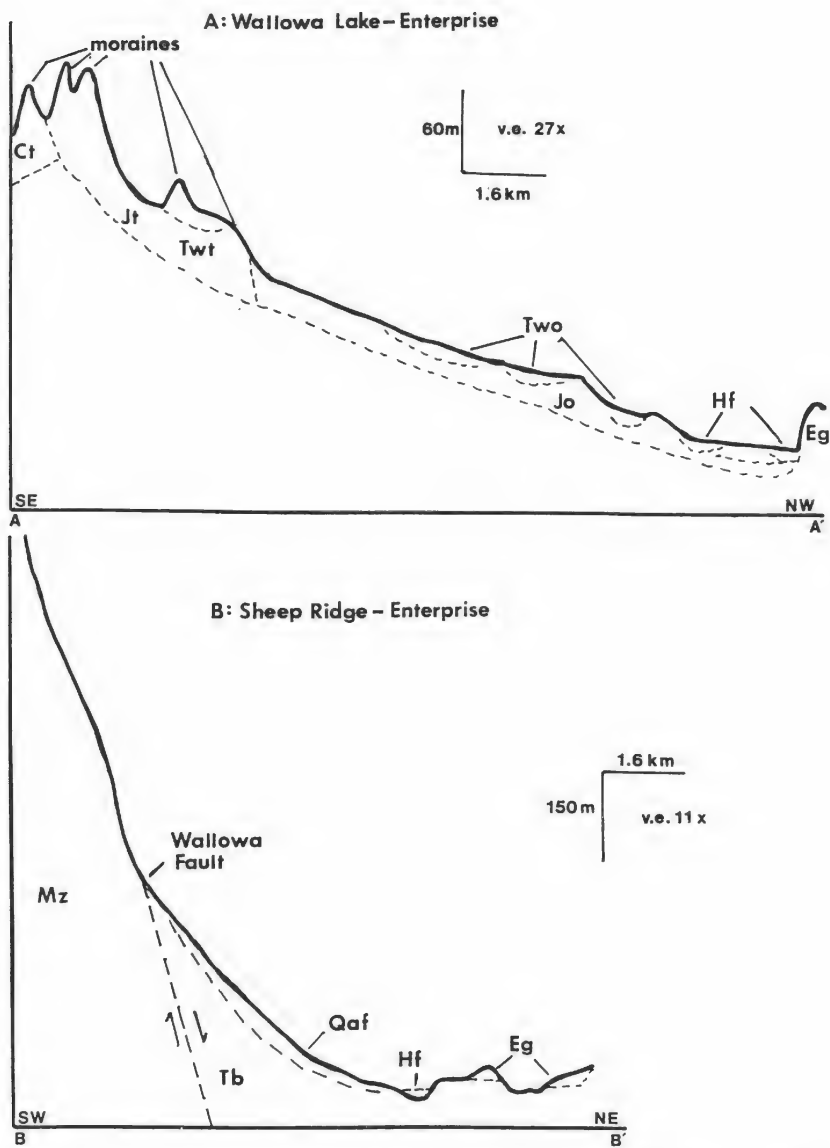


Figure 2. Cross-sections showing topographic relationships between the Enterprise Gravel and surrounding region. 2A (section A-A', Figure 1): From moraine complex at Wallowa Lake to type locality of Enterprise Gravel (drift units those of Crandell, 1967; EG-Enterprise Gravel; HF-Holocene floodplain). 2B (section B-B', Figure 1): From Sheep Ridge, Wallowa Mountains, to north of type locality of Enterprise Gravel (EG-Enterprise Gravel; HF-Holocene floodplain; Qaf-Quaternary alluvial fans; Tb-Columbia River Basalt Group; Mz-Mesozoic rocks).

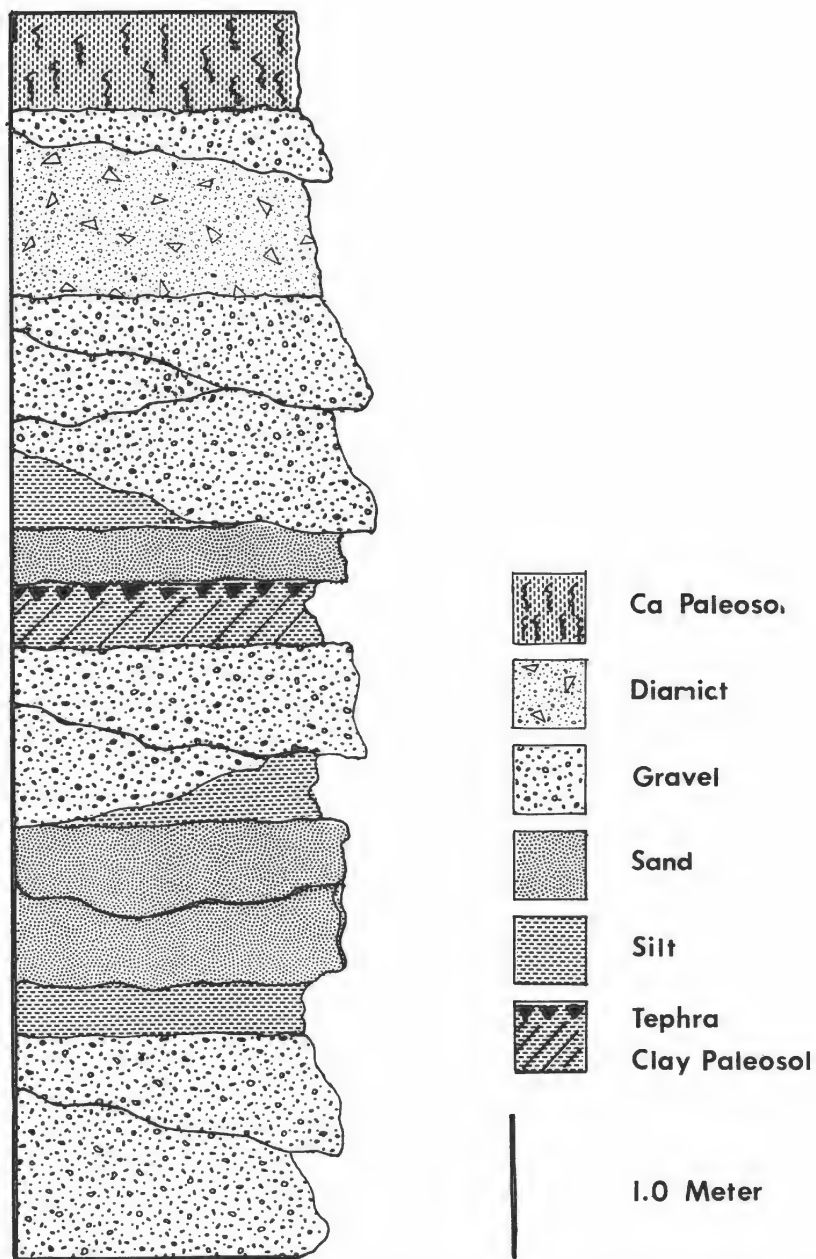


Figure 3. Idealized, composite stratigraphic column for the Enterprise Gravel showing facies relationships and location of Chief Joseph tephra.

Sedimentary Structures

Sedimentary structures in the Enterprise Gravel are numerous and diverse, the variety reaching a maximum at the type locality. Scour and fill features are abundant and associated with every depositional unit. Cross-stratification is common in the sandy intervals and present in some of the gravelly units. Parallel stratification is also well-developed in some of the sandy and gravelly units. Many of the gravel, diamict, and silt beds are massive.

At other localities, variability in the types of structures represented is minimal. Generally these supplementary sections display massive gravel beds, with scour and fill features well-developed, and massive diamicts. Cross-stratification is developed in the sandy intervals. Rip-up clasts of silt and fine sand are present in most sections.

Sedimentary Textures

Grain Size and Sorting: Except for the CJt and the paleosol, facies of the Enterprise Gravel are poorly sorted. Gravel units range in grain size from pebbles to cobbles with a coarse sandy matrix. Sandy intervals range from medium sand to granules and pebbles commonly with silt. Silty units range from medium and fine silt to medium sand. The diamicts contain pebbles and cobbles and are matrix-supported.

Grain Shape: The granular facies of the Enterprise Gravel exhibit well-rounded clasts. Diamict facies exhibit both angular and rounded clasts.

Contacts

The Enterprise Gravel rests unconformably upon the Miocene Columbia River Basalt Group. This contact can be observed at the type locality west of Enterprise. At other localities the basal contact cannot be observed, but can be inferred by the presence in close proximity of exposures of Enterprise Gravel and Columbia River Basalt.

The upper contact, marked by a well-developed pedocal, represents a period of non-deposition and soil formation. At the type and other localities, this soil is overlain by late Quaternary loess.

Clast Lithology

Clast counts of Enterprise Gravel were conducted at five gravel pits (Pinney *et al.*, 1986) to determine the provenance, whether the Wallowa Moun-

tains to the southwest, or the exposed basalt in the Joseph Upland to the north. At each pit, multiple beds were sampled. Data are summarized in Figure 4.

Three categories reflect lithologic types that predominate in the region: basalt, metamorphic and metasedimentary, and intrusive. Basalt is exposed north of the study area and capping the high peaks of the northern Wallowa Mountains (Walker, 1977, 1979). Also exposed in the Wallowa Mountains are late Mesozoic intrusive rocks, and a diverse suite of older Mesozoic and Paleozoic metamorphic (mostly greenstone and marble) and sedimentary rocks (mostly sandstone, siltstone, shale, and limestone) (Walker, 1977, 1979; Armstrong *et al.*, 1977; Armstrong, 1978; Brooks and Vallier, 1978).

Pebble count data shows a predominance of basalt and metasedimentary clasts in most exposures of the Enterprise Gravel, and an anomalously low proportion of intrusive rocks. Although this could reflect the fact that the intrusives were relatively recently unroofed by fluvial and glacial processes, it is more likely a reflection of the widely-spaced joint sets developed in the intrusive rocks, which would produce clasts too large to be transported as outwash.

Paleocurrent Indicators

The azimuth of inclination of cross strata was measured at seven different localities in the Enterprise Gravel (A-G, Figure 1). Localities A, B, C, and F, representing terrace remnants adjacent to the late Pleistocene outwash plain, show the most variation in paleocurrent direction, and suggest a depositional mode of constantly and randomly shifting current directions. Those localities along the modern Trout Creek valley (D, G, and E) indicate a variable-direction current, but preferentially to the north.

These data are consistent with pebble count data suggesting a source area in the Wallowa Mountains, with sediment spread northward from Wallowa Lake, and additional sediment from the Wallows distributed via the alluvial fans at the foot of Sheep Ridge across the area in various directions. Sediment found in the Trout Creek valley was confined to the valley and shows north paleocurrent dominance along the valley axis.

The paleocurrent data is consistent with modern drainage patterns on the late Pleistocene

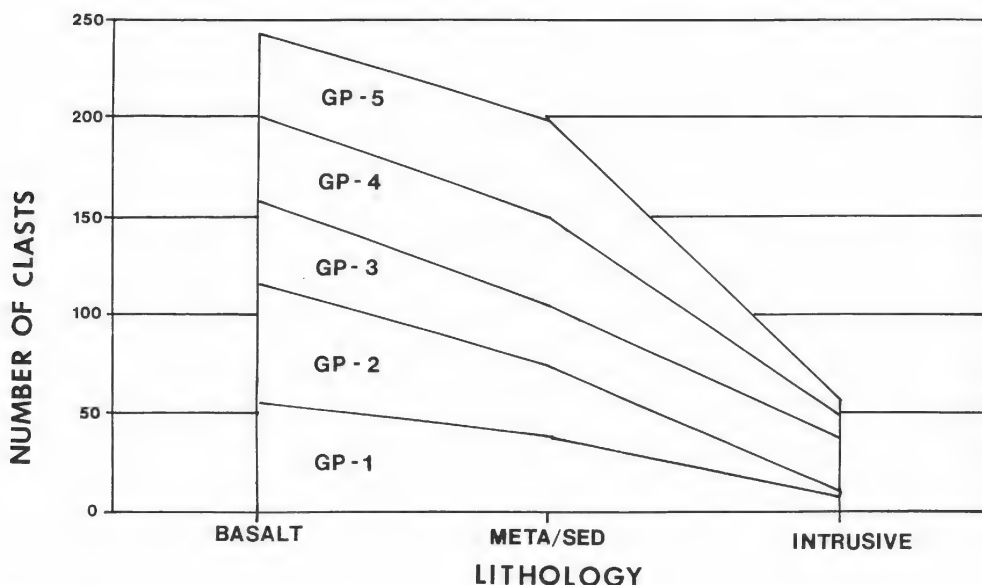


Figure 4. Summary of pebble count data (GP-1 through GP-5: gravel pits). Locations shown on Figure 1 (1-5).

outwash plain and alluvial fans. But Trout Creek presently drains the Joseph Upland in a southwestward direction to the west of Enterprise, where it joins the Wallowa River and flows northwestward. The paleocurrent data, with a predominant northerly component along Trout Creek, opposes the modern drainage and suggests that since deposition of the Enterprise Gravel, drainage in the Trout Creek valley has reversed. This relation was mentioned by Newcomb (1969); he attributed the reversal in drainage direction to downwarping of the syncline in which the modern Wallowa River flows, resulting in capture of the drainages of formerly north-flowing streams.

Depositional Mode of the Enterprise Gravel

Grain-size distribution of the sediment of the Enterprise Gravel, varying from silt through cobbles, suggests a depositional system characterized by variable energy conditions from relatively high (minimum transport velocity 1 m/sec) to nearly zero for fine-grained units. The absence of clay in the samples suggests that while energy was low at times, there was enough current to keep the finest material in suspension. The dominance of coarser sediments at most localities suggests that overall,

the depositional mechanism of the Enterprise Gravel was characterized by high energy.

Variation in paleocurrents suggests randomly and constantly shifting current direction: highly variable where unconfined by topography south of Enterprise but less variable where confined by topography in the Trout Creek valley.

Massive beds, trough cross-stratification, rip-up clasts, and abundant scour and fill features suggest rapid deposition of sediments as well as active erosion. Diamicts at many exposures of the Enterprise Gravel reflect periodic contribution of catastrophic events of rapid deposition, probably mudflows. These could have been introduced into the Enterprise Gravel via the alluvial fans of the Alder Slope, or as sediment derived from moraine bursts or jökulhlaups at Wallowa Lake.

The Enterprise Gravel represents a braided stream complex associated with a glaciofluvial environment. The subenvironments represented at the type locality are those of coarse-grained channel bars (gravel and sand), inactive channels and backwaters (silt), and exposed interchannel areas (B-horizon soil and root casts). At other localities, subenvironments represented include channels and channel-bars.

We propose that the Enterprise Gravel represents the deposits laid down by the ancestral

Wallowa River flowing northward from Wallowa Lake across the Joseph Upland to the Grande Ronde River.

Age of the Enterprise Gravel

Relative Age Criteria

Weathering rind thickness was measured on 79 clasts of basaltic composition from the terrace surface at the type locality. The mean weathering rind thickness is 0.3 mm (sigma = ± 0.3 mm). Comparison of this mean with results obtained by Colman and Pierce (1981) suggests an age of 20,000 to 40,000 years. Colman and Pierce (1981, p. 14) suggest that "the development of rinds is inhibited in dry, continental climates, especially where calcium carbonate accumulates within the soil." The age of the Enterprise Gravel is probably greater than indicated by data from the basalt weathering rinds.

Absolute Age Criteria

Magnetic Polarity

The CJt was analyzed in the field using a portable specimen magnetometer. In addition, a sample was excavated and laboratory paleomagnetic analysis was performed (Easterbrook, pers. comm.). Both field and laboratory analyses yielded a reversed magnetic signature (Spencer *et al.*, 1989). The most recent reversed polarity epoch was from 2.43 to 0.7 Ma; therefore the CJt is probably at least 700 Ka.

Fission Track

The CJt was processed for zircon grains to obtain a fission track age. The CJt is zircon poor, but enough grains were extracted to obtain a reasonable age.

The total age range of zircons from the CJt was from >8 Ma to about 1.8 Ma. The oldest grains were most likely accidental, and were disregarded. Fission track analysis of seven grains presumed to be primary give an age of 3.0 Ma (± 0.9 , 2 sigma). Figure 5a, showing the individual curves for seven grains, shows two clusters of curves; one of these centers on an age of 3.65 Ma, the second on 1.9 Ma. Two possibilities can explain these data: first, that there was a major volcanic eruption at about 3.0 Ma; second, that there were two eruptions, one at 3.65 Ma that provided accessory grains for a second eruption at 1.9 Ma.

The youngest cluster of essential grains indicates a minimum age for the Chief Joseph tephra and thus the Enterprise Gravel, of 1.9 Ma (± 1.1 , 2 sigma), or late Pliocene to middle Pleistocene (Spencer *et al.*, 1989). Paleomagnetic data further constrain the age to a reversed polarity interval, most likely the Matuyama Reversed Polarity Epoch (ca. 2.43-0.7 Ma) (Figure 6).

Fauna

At the type locality of the Enterprise Gravel, a diverse and well-preserved vertebrate fauna has been recovered (Spencer *et al.*, 1985). Aspects of its preservation were discussed by Spencer and Barnosky (1986).

The fauna comprises an assemblage of large and small vertebrates, including partial remains of a perissodactyl (*Equus*), a suid (wild pig), at least one carnivore tooth (*Canis*?), numerous small mammal bones, and at least one bird bone. Other localities in the Enterprise Gravel have not produced fossils, except for locality G (Figure 1) where a large scapula was recovered; based on its size, it is probably a mammoth or mastodon.

The fossils, particularly the perissodactyl, are in exceedingly good condition, despite the fact that they were recovered from diamicts overlying gravel. Many of the individual fossil elements display no evidence for post-mortem transport or abrasion, or post-burial dissolution or weathering (Spencer and Barnosky, 1986).

The primary significance of the fauna of the Enterprise Gravel is that it represents the first well-documented vertebrate fauna in the region, and thus may establish a standard for correlation with similar-aged deposits elsewhere in the West. Fission-track and paleomagnetic data on the CJt establishes the age of the Enterprise Gravel as late Pliocene to middle Pleistocene; the fauna may thus be assigned to the late Blancan to early Irvingtonian land mammal stages. Based on data in Kurten and Anderson (1980), the Enterprise fauna represents the only vertebrate fauna of Blancan or Irvingtonian age in the state of Oregon, and one of few in the greater Pacific Northwest region.

Tectonic History of the Enterprise Gravel

The Enterprise Gravel was deposited by the ancestral Wallowa River flowing north along Trout Creek valley. The gradient of the modern Wallowa River is 9 m/km from Enterprise 15 km northwest

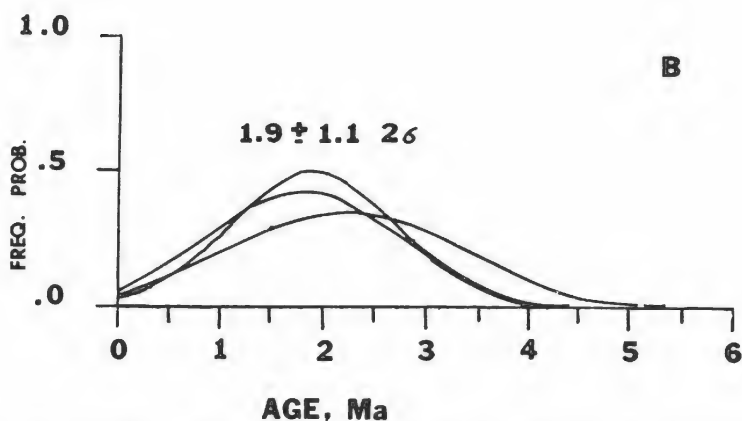
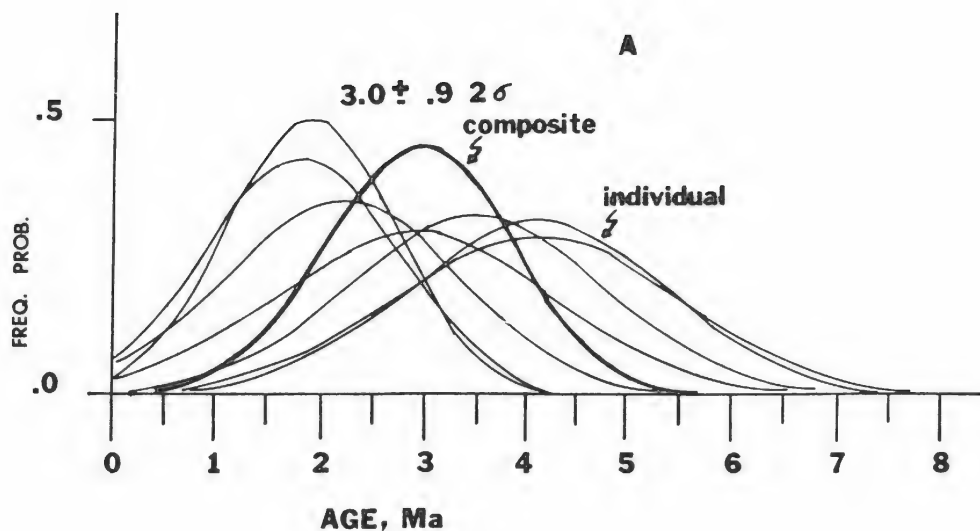


Figure 5. Summary of fission track data from the Chief Joseph tephra at the type locality of the Enterprise Gravel. 5A: Frequency probability curves for seven grains with composite curve and indicated age-range. 5B: Frequency probability curves for three grains clustered at low end of age-range, indicating minimum age for Enterprise Gravel of mid-Pleistocene.

to Lostine—approximately the gradient expected for the Enterprise Gravel between the type locality at Enterprise and gravel pit E (Figure 1). The slope of the upper surface (paleosol) of the Enter-

prise Gravel is 5.6 m/km southward along Trout Creek valley. The slope of the contact between the basalt and the Enterprise Gravel was not observed. If the original grade of the ancestral Wallowa River

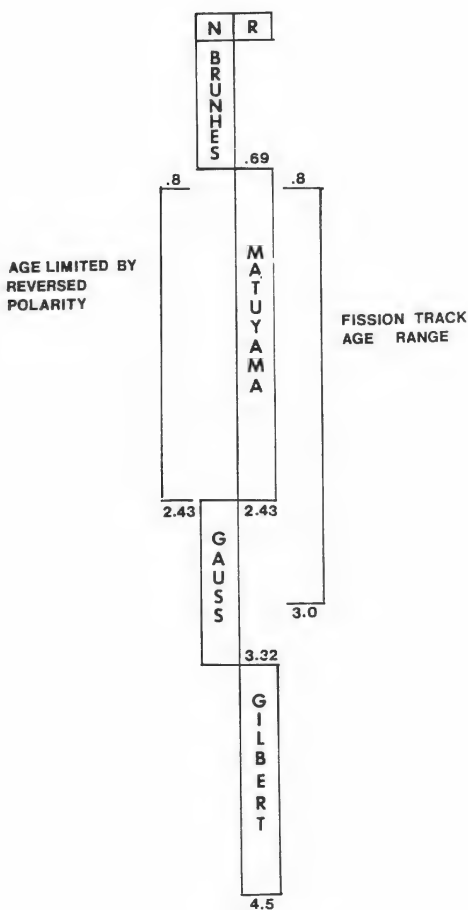


Figure 6. Summary of fission track and magnetic polarity data from the Chief Joseph tephra at the type locality of the Enterprise Gravel. Age of 2.43-0.8 Ma suggested by minimum fission track age and reversed magnetic polarity.

was 9 m/km northward, the Enterprise Gravel (and therefore the northern part of the Joseph Upland) has been tilted southward about 15 m/km since the late Pliocene or early Pleistocene. The northward paleocurrent indicators of the Enterprise Gravel contrast with the southward flow of the modern Trout Creek.

There was considerable tectonism in the Wallowa Mountains during the Cenozoic. Well to the north of Enterprise the anticlinal uplift of the Blue Mountains occurred, and just south of Enterprise,

the Wallowa Mountains rose along the Wallowa Fault. The Wallowa Fault runs along the base of the northeast side of the Wallowa Mountains, and flanks the study area on the southwest. This fault is part of the Olympic-Wallowa lineament (as defined by Raisz, 1945), which extends northwest from the Wallawas across Washington.

The altitude of the top of the Columbia River Basalt Group atop Sheep Ridge compared to that on the adjacent Joseph Upland, indicates movement along the Wallowa Fault of at least 1500 m vertically since Miocene time. But Imnaha Basalt flows (c. 17 Ma) are exposed atop the Wallowa Mountains, whereas Grande Ronde Basalt flows (c. 16 Ma; stratigraphically above the Imnaha) crop out in the Joseph Upland (Steve Reidel, pers. comm.). Vertical displacement may be closer to 2 km.

According to Newcomb (1969), deformation of the south part of the Joseph Upland was a result of downwarping of a suspected syncline, whose axis trends northwest along the course of the Wallowa River. There are, however, several possible explanations for the drainage reversal of the ancestral Wallowa River.

A. Synclinal downwarping of the Wallowa Valley and anticlinal uplift of the Joseph Upland (Newcomb, 1969).

B. Graben development in the Wallowa Valley. The Wallowa Fault forms the southwest border of the graben. According to Steve Reidel (pers. comm.), digital photography suggests the presence of an east-west trending, down-to-the-south fault between Enterprise and the Joseph Upland, which may be a splay of the Olympic-Wallowa Lineament.

C. Down-to-the-south step faulting between the Wallowa Valley and the Joseph Upland.

D. Listric faulting along the Wallowa Fault resulting in rotation (southward tilt) of the Joseph Upland.

It is unclear which relationship exists. Any combination of tilting, folding, and faulting resulting in the relative uplift of the Joseph Upland would have reduced the gradient of the ancestral Wallowa River and increased the likelihood of stream capture and drainage reversal. The canyon of the Grande Ronde River with its well-developed incised meanders indicates substantial late Cenozoic uplift of the Joseph Upland.

Within the area of the terrace segments and exposures of the Enterprise Gravel there is no field evidence for down-to-the-south faulting. Elevations of the carbonate-capped terrace segments indicate down-to-the-south tilting. As the north flow of the ancestral Wallowa River was being defeated by whatever mechanism, it was captured by a tributary of the Grande Ronde River located in the depression just northeast of the Wallowa Fault. Once the Grande Ronde tributary captured the ancestral Wallowa River, it became the modern Wallowa River.

Summary

The Enterprise Gravel, as newly defined in this report, comprises a sequence of sediments including sand, silt, gravel, diamict, two ancient soils, and a tephra. The environment of deposition of these sediments seems to be that of a braided-stream complex derived from the glaciers which once occupied the Wallowa Lake area, and alluvial fans on the Alder Slope to the southwest of the study area. Transport of the sediments was northward. Reversal of drainage direction was caused by tilting that was likely related to faulting associated with the Olympic-Wallowa Lineament. The distribution of the Enterprise Gravel defines the course of the ancestral Wallowa River, which moved to its present course probably in the Pleistocene, resulting in capture of the predominantly northward-flowing streams.

References Cited

- Armstrong, R.L., Taubeneck, W.H., and Hales, P.O. (1977). Rb-Sr and K-Ar geochronometry of Mesozoic granitic rocks and their Sr isotopic composition, Oregon, Washington, and Idaho. *Geological Society of America Bulletin* 88:397-411.
- Armstrong, R.L. (1978). Cenozoic igneous history of the United States Cordillera from latitude 42 to 49 degrees north. In R.B. Smith and G.P. Eaton, eds., *Cenozoic tectonics and regional geophysics of the western Cordillera*. Geological Society of America Memoir 152:265-282.
- Baldwin, E.M. (1986). *Geology Of Oregon*. Kendall-Hunt Publishing Company, Dubuque, Iowa. 170p.
- Brooks, H.C., and Vallier, T.L. (1978). Mesozoic rocks and tectonic evolution of eastern Oregon and western Idaho. In "Mesozoic paleogeography of the western United States." (D.G. Howell and K.A. McDougall, Eds.), *Pacific Coast Paleogeography Symposium* 2:133-145.
- Colman, S.M., and Pierce, K.L. (1981). Weathering rinds on andesitic and basaltic stones as a Quaternary age indicator, western United States. *U.S. Geol. Surv. Prof. Pap.* 1210:56p.

The diamicts in the Enterprise Gravel indicate that catastrophic events of sedimentation, possibly related to moraine bursts or jökulhlaups at Wallowa Lake or mudflows from the humid alluvial fans to the west, periodically discharged large volumes of sediment instantaneously.

Fission track and paleomagnetic data loosely constrain the Enterprise Gravel to an age of late Pliocene to middle Pleistocene. The fauna of the Enterprise Gravel represents the first recorded occurrence of Blancan or Irvingtonian vertebrates in the state of Oregon, and one of few such sites in the greater Pacific Northwest region.

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- Crandell, D.R. (1967). *Glaciation at Wallowa Lake, Oregon*. United States Geological Survey Professional Paper 575-C:145-153.
- Kurten, B., and Anderson, E. (1980). *Pleistocene mammals of North America*. Columbia University Press, New York. 442p.
- Newcomb, R.C. (1969). *Geology of the Joseph Upland In "Mineral and water resources of Oregon."* (A.E. Wisenborn, Ed.), State of Oregon Department of Geology and Mineral Industries Bulletin 64:66-68.
- Pinney, D.S., Spencer, P.K., and Carson, R.J. (1986). Quaternary geology in the Enterprise, Oregon area: the ancestral Wallowa River and tectonism near the Olympic-Wallowa lineament. *Proceedings of the Oregon Academy of Science* 22:35.
- Raisz, E.J., (1945). The Olympic-Wallowa lineament. *Am. Jour. Sci.*, v. 243-A:479-485.
- Spencer, P.K., Carson, R.J. and Orr, W.N. (1985). Pleistocene vertebrates and sediments near Wallowa Lake, Oregon. *Geological Society of America Abstracts with Program* 17:6, 410.

- Spencer, P.K. and Barnosky, A.D. (1986). Taphonomy of a Pleistocene vertebrate fossil assemblage. Geological Society of America Abstracts with Program 17:7, 723.
- Spencer, P.K., Carson, R.J., Tabbutt, K.D., and Easterbrook, D.J. (1989). Age of the Enterprise gravels, Wallowa Lake, northeastern Oregon. Geological Society of America Abstracts with Program 21:5, 147.
- Walker, G.W. (1977). Geologic map of Oregon east of the 121st meridian. United States Geological Survey Miscellaneous Investigation Series Map I-902.
- Walker, G.W. (1979). Reconnaissance geologic map of the Oregon part of the Grangeville quadrangle, Baker, Union, Umatilla, and Wallowa counties. United States Geological Survey Miscellaneous Investigation Series Map I-1116.

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Northwest Science Forum

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Jerry O. Wolff, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

On the Limitations of Species-Habitat Association Studies

A trend in wildlife ecology over the last 25 years has been to study characteristics of a species habitat, primarily vertebrate species of management concern, and then infer something about habitat preferences or suitability for that particular species (e.g. Verner *et al.* 1986). The approach includes identifying a relatively high density population of a given species, or in some cases documenting the home ranges of representative individuals from that population, and then correlating habitat use or daily activity patterns with a series of habitat measurements such as plant species composition, vegetation juxtaposition, topography, and so forth. Presumably, this correlation tells something about habitat preferences or suitability for the species. In many cases, the study stops here and is published simply with correlational results. More appropriately, the correlational results are used in wildlife-habitat association or habitat suitability index (HSI) models (Fish and Wildlife Service 1981; Verner *et al.* 1986). These models have their application if tested properly, but they too have their pitfalls and shortcomings (e.g. Laymon and Barrett 1986; and other references in Verner *et al.* 1986). Herein, I summarize what I see as some problems associated with the use of wildlife-habitat association studies as endpoints in themselves. I am not the first to point these out and I refer the reader to Ruggiero *et al.* (1988) and many of the

references in Verner *et al.* (1986) and Morrison *et al.* (1992) for further discussion. My arguments are of a general nature and I avoid citing specific studies to make a point. My intention is not to denounce all habitat-association studies, but rather to caution investigators and managers of their pitfalls and limitations. In doing so, I emphasize the importance of understanding behavioral as well as ecological factors that determine a species distribution.

1. The wildlife-habitat correlational approach does not provide an endpoint in itself. Wildlife habitat association studies are conducted where a species is known to occur; therefore, some positive correlations are likely to be derived for that species and some particular habitat feature(s). This type of study provides only the baseline data necessary to predict where a species *can* occur. Two additional components are required to make the study conclusive and the results predictive. First, to verify the relevance of these habitat correlates to the presence of the species, the study must document that the species does not occur in other randomly selected areas where these habitat features do not exist. Second, the study must test the now *a priori* predictions that the species will occur in habitats where these features are present and not in areas where they are not (i.e. the retrospective correlational study now becomes prospective). This

testing of the model can be done through natural experiments by finding similar habitats that do and do not have these same key features or through manipulation and experimentation (see references in Verner *et al.* 1986 for results of attempts to validate models). This last part of the study, and in some cases the latter two parts, are often not done. Therefore, the species-habitat correlation part of the study is left incomplete. Without the latter two parts the study, managers can not make defensible predictions or conclusions, or have confidence in management decisions. I might point out that management agencies are very good at funding the first of the series, but almost never fund the validation studies. The lack of validation causes uncertainty and may ultimately result in loss of credibility of biologists.

2. Species ranges of tolerance are often greater than can be measured in one short-term localized study. The historic distribution records of vertebrate species shows that most species at one time had much greater ranges than they have today. Most species of management concern have a much wider range of ecological tolerances than can be described in one isolated subpopulation. We also know that many of these species live in a variety of macro- and microhabitats (consider for example the variety of habitats in which elk, *Cervus elaphus*, marten, *Martes americana*, Douglas squirrels, *Tamiasciurus douglasii*, and red-tailed hawks, *Buteo jamaicensis*, occur). Therefore, species-habitat correlations determined from only a few individuals from a subpopulation in a small part of the species range tells us virtually nothing about the range of tolerance for that species throughout its distribution. In this sense, species-habitat association studies are not species-level studies, but rather subpopulation-level studies. Species obviously survive very well outside the range of any habitat measurements made in a specific subpopulation-habitat association study. Thus, the results may be relevant for the particular study site examined and not much beyond that (but see Noon *et al.* 1980). The result, therefore, has little, if any, predictive power for the species, yet is often accepted as factual and conclusive and applied to the species in other parts of its range. This may be an inappropriate application of these results, especially for species with wide distributions that exhibit ecotypic variation which may or may not be genetic adaptations to localized conditions.

3. The results from species-habitat association studies are often interpreted to mean that the species does not or cannot exist in areas where these selected habitat features do not exist. In other words, presumably all the "good" habitat is utilized and to increase numbers of individuals or population size, more of this good habitat should be created. This may not be a valid assumption for at least two reasons. First, many species now survive in refugia habitat that remains after humans exploited much of the habitat previously occupied by the species. Therefore, a given species may be existing in marginal and not optimal habitat, because optimal habitat no longer exists. Second, consider for example the Ideal Free Distribution Model of Fretwell and Lucas (1970) which proposes that animals first settle in "optimal" habitats and then as these territories become occupied, additional individuals settle in "suboptimal" or "marginal" areas. The reproductive success of individuals in suboptimal or marginal areas may be just as good as those in optimal areas for a variety of reasons. On the other hand, the Ideal Dominance Distribution (Fretwell 1972) and Source-Sink Models (Wolff 1982, Pulliam and Danielson 1991) do have survival and fitness consequences for individuals in optimal, suboptimal, and marginal habitats. Some measure of fitness is thus necessary to conclude something about habitat quality (see also number 10 below). Similarly, species-habitat association measurements focus on a very short-term time frame, often less than one year, and do not consider multi-annual, or in some cases even seasonal variation in habitat use, or lifespan of the species (voles, *Microtus*, versus elephants, *Loxodonta*, versus migratory caribou, *Rangifer tarandus*).

A related assumption often made in species-habitat association studies is that the population is at carrying capacity, in "optimal" habitat, and is relatively constant in time and space. This assumption too is often invalid and probably never tested. For instance, habitat and/or nest-site selection may vary temporally and spatially especially for predators that feed on fluctuating prey such as lemmings, *Lemmus lemmus*, or snowshoe hares, *Lepus americanus*, or for nesting birds in the presence or absence of predators. A perfect or even "optimal" habitat probably does not exist for any species, but rather most species are flexible in their requirements and adjust to variable ecological conditions. Habitat association studies should focus

more on the limitations for a given species than on studying populations where they do "best." Limitations as well as "best" must be defined in terms of survival and reproductive success.

4. A problem exists with independence of observations and lack of replication. Although some studies have used replicate plots that are independent of each other, most studies use individuals rather than plots as replicates. In the case of social animals such as deer, *Odocoileus* sp., and elk, the movements and habitat use of one individual are not independent of those of another individual in the same social unit, such as a mated pair, mother and offspring, or members of the same harem. In territorial species, the position of each territory is influenced by the boundary of an adjacent individual (i.e. no two individuals can occupy the "preferred" space). In mammals, the space used by males may be more dependent on the spacing of females than any specific habitat feature. For large herbivores such as deer, elk, and caribou, males associate with females only during a short breeding season, whereas during the non-breeding season, the sexes are segregated, often in very distinct habitats. In small mammals with long breeding seasons, males select habitat based on the proximity of estrus females. In birds, males establish territories and females choose males based on their territory. Therefore, habitat selection or preferences of males and females that have contiguous or overlapping home ranges are not independent of each other and can not be used as independent observations for statistical purposes. Similarly, for species that exhibit seasonal segregation of the sexes, each sex, habitat, and season must be considered separately. This is rarely done.

5. What does "habitat preference" really mean to the individual animal. Just because an individual spends more time in one habitat than expected, based on the habitat's frequency of occurrence (= preference), says nothing about how critical that habitat is for survival and reproduction. For instance, marten spend 95% of their time in forest habitat, but a very critical 5% of their time hunting voles in adjacent grassland habitat (Spencer 1981; Zielinski 1981). Likewise, many owls require large trees for nesting and adjacent open fields for foraging. Therefore, habitat requirements may include a mosaic of habitat types and the juxtaposition of habitat patches to one another is what is important, not the time spent in each habitat type. Similarly, deer and elk often seek shel-

ter in forests and forage in edge or open areas. The time spent in each habitat is irrelevant to the importance of each. Habitat "preference" for snowshoe hares is determined by predator pressure, not optimal food conditions; distribution of moose, *Alces alces*, may be limited by interspecific interactions with white-tailed deer, *Odocoileus virginianus*; and habitat use by red-winged blackbirds, *Agelaius phoeniceus*, varies depending on the presence or absence of yellow-headed blackbirds, *Xanthocephalus xanthocephalus*. Habitat preference is often used as a mathematical and not a biological measure of importance or preference (Porter and Church 1987).

6. Species habitat association studies do not take advantage of the scientific method for conducting research. The scientific method has six parts; (1) make an observation (or documentation from the literature), (2) list all reasonable alternative hypotheses that could explain this observation, (3) design an experiment (observational or manipulative) that allows for rejection of each hypothesis independently, (4) conduct the experiment (or gather the data), (5) analyze data, and (6) draw conclusions. The species-habitat association studies do not test hypotheses. More importantly they are not designed to reject alternative hypotheses. Species-habitat association studies use a reductionist approach to look for positive correlations with one or a few habitat features and do not address alternative explanations for the observation. Research projects that have *a priori* hypotheses that are rejectable with the data gathered in the study make a greater contribution to science than do correlational studies that do not provide a basis to reject alternatives.

7. Species-habitat association studies ask the wrong question. These studies are descriptive and address the "what," or proximate mechanisms questions rather than "why" or ultimate causes questions (Gavin 1991). The question should be not only "what," but "why" certain factors determine the distribution of a given species (or more importantly, determine survival and reproductive success). The requirements for life for any species include physiological adaptations to the abiotic environment, ecological adaptations to the biotic environment, and behavioral adaptations to the social environment. Therefore the questions are, (1) is the species physiologically adapted for a given habitat (environment), (2) can it find enough food on which to live, (3) can it survive (avoid predators

and competitors), and (4) can it find a mate and nest site and breed successfully? Once these questions are answered, the conclusions have direct application to management or any other scientific objective. The correlation of a few individuals in a subpopulation in a small portion of the species' total range to a few habitat structural features might prove quite insignificant and irrelevant once these four questions are answered.

8. Correlational studies cannot demonstrate cause and effect. In the case of habitat features, these measurements supposedly indirectly measure predator avoidance and access to food and shelter, though this is rarely demonstrated (but see references in Verner *et al.* 1986). A real danger exists in making use of indirect measures where results can often be misleading. For instance, take an analogous situation. If I were to place radio-transmitters on 30 biologists and follow them around for three months, I might conclude that their use of habitats includes 30% time in brick buildings, 30% in wooden buildings, 20% outdoors, 10% in motor vehicles, and 10% other. This tells me nothing at all about where the biologists find food (access to resources), avoid predators or competitors (seek shelter), or seek mates and rear offspring (maximize their fitness). If the grocery store moved from a brick to a steel building or a biologist transferred from an indoor administrative position to an outdoor field laboratory, the results would be invalidated. Whereas, if my objectives were to predict that the 30 biologists will occur where they have access to resources (food and shelter = employment) and mates, I would have direct measurements of individual needs and results that were predictive. If I could measure reproductive success of each individual and correlate it with the habitat variables measured, I would have the ultimate measure of the importance of the different variables. If I wanted to ask where a species *could* live, I would be better off measuring a food source, shelter, and presence of predators or competitors, than I would measuring diameters of trees or percent ground cover of moss or logs. These latter measurements are only valuable if I have statistical confidence in how they relate to the former factors through time and space.

9. Habitat-association studies focus on a species' ecological surroundings and do not consider the evolutionary or behavioral aspects of why animals do what they do (Gavin 1991). A sound theoretical base is available for

asking questions based on the functional significance of space use. For instance, theories on aggression and territorial defense, mate selection, parental strategies, and optimal foraging behavior predict that home range size, shape, and defense should shift seasonally with respect to availability of different food resources, access to mates, protection of young from infanticide, and vulnerability to predators (Krebs and Davies 1993). Questions asked in species-habitat association studies are about the species, whereas selection for these traits acts on individuals and not species or even subpopulations. Also, an application of evolutionarily stable strategy theory (Maynard Smith 1982) to habitat or nest site selection would place the results within the framework of natural selection.

10. Wildlife habitat-association studies do not measure fitness. Darwin's theory of evolution by natural selection is the central and unifying paradigm for all the life sciences. The only true measure that is relevant in any ecological study on a species is fitness, one that is overlooked in habitat-association studies. Although this measurement is difficult to get, it is not impossible and should be attempted whenever possible. Whether a species exists in old growth forests, pole size-class timber, north- or south-facing slopes, or coniferous or deciduous forests, if individuals are surviving and reproducing at the same rate as in "preferred" habitat, then any habitat-association measure is superfluous. Species are often much more resilient and adaptable than can be interpreted from a few habitat measurements. I do not doubt that most, if not all, species could expand their range and use more of existing habitats if they were not disturbed or preyed upon by humans. Therefore, some measure of human activity or disturbance is probably much more meaningful than is some measure of habitat variables.

I strongly encourage vertebrate biologists to consider "what is the question" before they embark on a detailed methodology that has limited application to the endpoint desired. Researchers must define the goal of a species-habitat association study. Is it to predict occurrence? to choose "best" habitats for preservation or management? to provide baseline data to manipulate or create wildlife habitat? to describe patterns or explain processes? or what? A good clear objective, set of testable hypotheses, and appropriate methodology will lend predictability and applicability to the

results. In that the future of many wild populations is in jeopardy, precise and conclusive research on wildlife habitat is essential for continued preservation of threatened species and ecosystems. Perhaps measures of the functional relationship of biotic, abiotic, and social environments will provide a sound basis for accomplishing these goals. I hope this comment will be seen in light of contributing to this goal.

Literature Cited

- Fish and Wildlife Service. 1981. Standards for the development of suitability index models. Ecol. Services Manual 103. U.S. Fish Wildl. Serv., Division of Ecological Services. Government Printing Office, Washington D.C.
- Fretwell, S. D. 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton.
- Fretwell, S. D. and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta. Biotheor.* 19:16-36.
- Gavin, T. A. 1991. Why ask "why": the importance of evolutionary biology in wildlife science. *J. Wildl. Manage.* 55:760-766.
- Krebs, J. R. and N. B. Davies. 1993(3rd edition). *An Introduction to Behavioural Ecology*. Blackwell Scientific Publ., Oxford.
- Laymon, S. A. and R. H. Barrett. 1986. Developing and testing habitat-capability models: pitfalls and recommendations. *In* J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000 Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison. Pp. 87-91.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Morrison, M. L., Marcot, B. G., and Mannan, R. W. 1992. *Wildlife-habitat relationships*. University of Wisconsin Press, Madison.

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- Noon, B. R., D. K. Dawson, D. N. Inkley, C. S. Robbins, and S. H. Anderson. 1980. Consistency in habitat preference of forest bird species. *Trans. N. Amer. Wildl. Nat. Res. Conf.* 45:226-244.
- Porter, W. F. and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. *J. Wildl. Manage.* 51:681-685.
- Pulliam, H. R. and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective. *Am. Nat.* 137:s50-s66.
- Ruggiero, L. F., K. B. Aubry, R. S. Holthausen, J. W. Thomas, B. G. Marcot, and E. C. Meslow. 1988. Ecological dependency: The concept and its implications for research and management. *In* R. E. McCabe, ed. *Trans. 53rd N. Amer. Wildl. & Nat. Res. Conf.* Pp 115-126.
- Spencer, W. D. 1981. Pine marten habitat preferences at Sagehen Creek, California. unpubl. M.S. Thesis, Univ. Calif., Berkeley.
- Verner, J., M. L. Morrison, and C. J. Ralph, eds. 1986. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison.
- Wolff, J. O. 1982. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. *In* K. Myers and C. D. MacInnes, eds. *Proc. World Lagomorph Conf.*, University of Guelph, Ontario. Pp. 441-449.
- Zielinski, W. J. 1981. Food habits, activity patterns, and ectoparasites of the pine martin at Sagehen Creek, California. unpubl. M.S. thesis, Univ. Calif., Berkeley.

Book Reviews

Mountain Environments & Geographic Information Systems

Martin F. Price and D. Ian Heywood. Taylor and Francis, London. (1994)

The editors have organized this compilation of international papers into a cohesive flow of information useful for those experienced in Geographic Information System (GIS) applications, as well as people more interested in the subject of mountain environments themselves. The focus of mountain environments for GIS applications provides an excellent framework for those just wishing to learn more about GIS technology.

Like the environments discussed in this book, GIS technology is not one simple set of tools, but rather, a complex and often perplexing array of tools in a continuous state of evolution. The complexity of GIS permits the use of the technology in diverse applications. These can be as diverse as planning the use of urban utilities, to mapping the potential effects of global environmental change. However, the complexity of most current GIS technology often limits the use and understanding of GIS applications. In this book, the complexity is reduced by limiting the discussion to a subset of potential GIS applications. The features of mountain environments provide a natural focus for understanding the capabilities and applications of GIS technology. As mentioned by the authors, the investigations described in the book may not always represent the state of the art, but give actual results using GIS technology, rather than only suggestions of potential applications.

Just as the specific applications of GIS to mountain environments are explained, the capabilities of GIS are an integral part of the chapters. This book uses the focus of mountain environments to explain how GIS systems work. The structure and content of the book chapters provide an important flow of information. The layout of the book eases nontechnically oriented people into the applications of GIS by giving a general introduction, and walking the reader in a logical progression through the GIS applications. The GIS applications are examples of current research associated with mountain environments. These include watershed management based on ecological modeling, land use clas-

sification and regional planning, natural hazards including fire prediction, research and management of protected areas, analysis of deforestation, and the impact of climate on local and regional ecosystems. The international perspective provides an important diversity to these applications.

The introductory chapter covers specific elements of mountain regions and their relation to aspects of GIS technology. The importance of considering the temporal and spatial scale in GIS analysis is stressed and related to the complex structure of mountain environments. After providing background for various applications of GIS in mountain environments, and explaining what type of information is important, a chapter is presented on how this type of information is used in various model scenarios for planning purposes. In a logical sequence, a chapter then explains important aspects of terrain analysis and provides information on how terrain data are generated for use in the GIS. This is followed by a chapter to explain a method of transforming integrated GIS data including, but not limited to, satellite remote sensing data. The process of classifying these data into thematic GIS information using current technology is explained. The chapter presents the advantages and limitations of the method used and provides the reader with an overall view of how "correct" such data are.

Chapters on specific applications of GIS to the mountain environment give examples of how GIS projects are managed. These include international perspectives from both academic and commercial levels. Applications of visual quality and viewsheds lead into applications of redevelopment, for example of past mining regions. Incorporating economic considerations related to topography for areas in Japan provide additional examples of GIS applications. This particular focus at the international scale demonstrates the need to include cultural values and recognize that these values may vary between international boundaries and with time. Incorporation of these cultural values is not unlike other subjective values that need to be included in statistical and model analysis.

The need for multidisciplinary approaches in GIS applications is evident in examples of assessment of landslides both in their causes and

their results. Causes of landslides can include earthquakes, rain, rain on snow events, associated floods, disturbances due to logging, road building and other activities. This emphasizes the importance of spatial scale in the specific applications. High resolution information is needed for specific applications such as stability of forest roads, while large scale, regional hazard data may be more important for applications of urban property protection, disaster potential or evacuation needs. A similar analysis of fire potential involves many issues linked to terrain analysis for determination of details such as forest fuel types and loads, moisture content and overall heterogeneity of potential fires. An excellent example of complex issues in spatial analysis and modeling is given in a chapter focused on Glacier National Park. A diversity of examples is used, from integration of climatic variables related to avalanche potential, to assessment of water turbidity in the alpine lakes. An excellent example of comparing model output of predicted vegetation at treeline with observed conditions from satellite information is given. In these examples, importance of integration of diverse information is emphasized, including that from satellite data. The methods for integration of satellite information, and the expertise that is involved, is perhaps underplayed in most of the examples listed.

An experience from the Wildlife Service of New South Wales points out an important problem associated with GIS use. The expertise required for actually using current GIS information is often quite high, as are costs associated with the hardware and software. By reducing the complexity and improving access to software and databases, the results of the GIS investigations and investments were applied on a much wider basis. This included field staff working with the data on the "ground level." On the other side, is the need to realize that specific research applications involving complex modeling and data integration are, by design complex. Several investigations are described in the chapters, which include the powerful features of GIS tools for modeling applications and integration of model output

from other analytical tools. These examples include spatial results with fractal analysis, deforestation rate and risk potential models, and use of models within the GIS for analysis of topographic influences, and further integration with climatic data. These studies also cover some results of scale dependencies, including limitations of the datasets.

Although a good introduction is given for the papers of the book, perhaps one weakness is a need for a concluding chapter. The applications presented in this book vary widely in scope and application. The complexities presented within the chapters of the book provide an opportunity for several approaches and conclusions. An important message conveyed in the forward of the book, but sometimes lost in later chapters, is a paradox that often exists in GIS applications: The technically oriented application of GIS technology is often needed for basic, non technical, bottom line results. This is implied in many of the chapters, but needs to be stressed. Complex analytic procedures often need to generate a simple yes or no answer. As part of this, the results may need to be conveyed to a nontechnical audience. To make it more difficult, even with advanced tools, satellite information and complex model output, many GIS applications need to include or rely on information of uncertain validity. This might include historical data of undocumented spatial accuracy or resolution, undocumented transformations, or even anecdotal information. The result of the analysis must include this level of uncertainty and must convey the meaning of this uncertainty to a nontechnical audience. The chapters of this book present excellent examples of the power of GIS in complex mountain environments, but GIS technology still needs a better interface for more widespread access to the digital information and results like those presented in these chapters.

—John Vande Castle
LTER Network Office
College of Forest Resources, AR-10
University of Washington
Seattle, Washington 98195

Killer Whales

John K. B. Ford, Graeme M. Ellis, and Kenneth C. Balcomb. University of British Columbia Press, Vancouver, British Columbia, Canada; and University of Washington Press, Seattle, Washington, USA.

Killer whales (*Orcinus orca*) may be the most recognizable and compelling symbols of marine wildlife and ecosystems in northwestern North America. They are of incalculable significance to the Native American cultures of the northwest. First-hand encounters with killer whales in the wild, especially at close range, are jaw-dropping experiences for even the most jaded observer, and provide an irresistible lure for thousands of tourists. The proximity of many killer whale populations to the coast, and their strong site fidelity, provide some of the best opportunities known for the scientific study of whale behavior and ecology. The controversial presence of killer whales as showcase performers in marine theme parks and aquaria has awakened generations of lay public to the wonders of marine mammals.

Two developments during the 1960s were particularly significant in bringing killer whales to the forefront of public and scientific awareness, where they remain to this day. The capture of a killer whale later known as "Namu," and his Barnum-esque display and promotion in Seattle, drew increased attention to killer whales and helped create a societal dilemma that remains unresolved: captive killer whales may be at risk of compromised health, and their removal from family groups may be immoral or unethical. However, the public display of captive killer whales serves to educate people about the animals, provides important opportunities for research and draws public attention toward marine conservation issues. Within a few years of Namu's capture, the *Torrey Canyon* oil spill off England and the *Platform A* oil spill off California accelerated the emergence of the marine environmental movement. With public consciousness sharply focused on coastal marine habitats, and killer whales an obvious and appealing symbol thereof, intensive investigation of killer whale biology seemed in order. Two problems remained. First, someone had to step forward and do the work. Second, and more daunting, a key was needed to unlock the challenge of studying rare, highly mobile animals that live primarily under water and are visible at the surface only a tiny fraction of the time.

Killer Whales is subtitled "The natural history and genealogy of *Orcinus orca* in British Columbia and Washington State." It is an updated version of a similar volume, published in 1987 by M. A. Bigg (since deceased) and the current authors. Following the pattern of the earlier edition, the book aspires to three goals: provide a synopsis of the natural history of killer whales; provide a history and guide to the identification of individual killer whales; and provide a genealogy of killer whales living near the coasts of British Columbia and Washington State. The target audiences for *Killer Whales* include scientists, amateur wildlife enthusiasts, and the interested lay public. The book is paperbound, in relatively large format, with several major sections. The introduction includes a verbatim reproduction of a passage written for the 1987 edition by Dr. Bigg, whom the authors warmly identify as a friend and mentor. Dr. Bigg had a pivotal role in developing the long-term study of northwest killer whales. Perhaps his most significant contribution was recognition, along with his associates, that killer whales carry distinctive natural markings on their backs and dorsal fins. The marks allow scientists to track whales as recognizable individuals, providing the key to the identification and analysis of killer whale societies and other ecological characteristics.

The major sections of the book cover natural history, characteristics of resident killer whale societies in the Northwest, pointers and etiquette for watching killer whales, and an extensive catalogue of individual killer whales. The latter includes nomenclatural definitions and genealogies, with separate photographs of over 300 individually recognizable whales. Interspersed among the various sections are inset-format passages that focus on whale-watching tours, ecological reserves, communication and echolocation, and other issues. There is a useful list of selected popular and technical publications about killer whales. The volume is extensively illustrated with diagrams and black and white photographs. The center portion of the book includes eight pages of color photographs. All photographs are clear, informative, and of good quality. The prose will hold the interest of the specialist, but will be easily assimilated by the lay reader, as well.

The heart of the volume is the description of social characteristics of northwest whales, and the catalogue of genealogy and photoidentification. These sections are clear, concise, and obviously

the focus of the authors' interest. I enjoyed the well-defined summaries of social organization, including the hierarchies of association, definitions of home ranges, and descriptions of resident, transient, and offshore forms. The understanding of killer whale social organization is a stimulating monument to the hard work of the authors, Dr. Bigg, and their colleagues. The catalogues of individual photographs are a significant resource for scientists interested in killer whales. Publication of the catalogues is a lasting contribution to the field.

The coverage of other important areas of natural history is uneven, and often rather thin. Given the stated aspirations of the authors, I was somewhat disappointed, for example, to find no photographs or diagrams of a killer whale skeleton or of the structures involved in sound production or reception. There is no discussion of the biological significance of sexual dimorphism in the dorsal fin, or of the harlequin skin coloration characteristic of the species. There seems to be a disproportionate focus on British Columbia whales and habitats at the expense of those to the south. Given that the book is intended, in part, for specialists, I would have hoped for a greater effort toward comparisons with known societal or ecological patterns in other well-known cetaceans such as the bottlenose dolphin, or with other intensively-studied social carnivores, such as hyenas, African lions, or wolves.

I found myself puzzled by some organization features of the book. Much of the discussion of echolocation and communication is relegated to a separate inset placed in the midst of the genealogical catalogue. The description of features that distinguish males and females is contained primarily in a marginal note near the beginning of the catalog section. I was surprised to find relationships of dialects among pods, clans, and communities represented in the form of a cluster diagram almost certain to confuse readers without a technical background. I found no typographical errors, and few errors of factual detail, although two are worth noting. The Soviet whaling data cited on page 12 almost certainly are in error, given recent revelations of widespread deception by the Soviets in reporting of catches. On page 57 the National Marine Fisheries Service (NMFS) is identified as the agency responsible for protection and management of marine mammals in U. S. waters. In fact the responsibility is divided between NMFS (cetaceans and all pinnipeds except walrus) and the U.S. Fish

and Wildlife Service (walrus, sea otters, manatees, dugongs, polar bears).

The volume makes a point of recognizing important issues yet to be resolved for killer whales. A good example is the unknown genetic linkage among resident, transient, and offshore whales. The provocative suggestion that these categories of whales may in fact represent distinct subspecies should stir the minds of marine mammal biologists, and stimulate important new investigations. In some cases, however, the lay reader may find it difficult to distinguish established fact from the authors' speculations about untested hypotheses. A good example is the discussion on page 21 of the genealogical significance of acoustic dialects.

I found the book difficult to categorize with regard to the goals of the authors. As a natural history, it is incomplete. As a field guide, it may be physically unwieldy and quite unlikely to survive the rain, mist, and sea spray that typifies the realm of killer whales. Moreover, the care and discretion necessary for photoidentification in the field may be beyond the patience and skill of most weekend naturalists. As a "coffee table book" for the armchair naturalist, it may be underproduced and too brief. As a technical treatise, it lacks the necessary rigor, cross-species perspective, quantitative analyses, and referencing. *Killer Whales* is, however, an attractive, informative, and stimulating volume that I will recommend to my family, friends, and colleagues, and require of my students. That it defies categorization may simply reflect the unusual focus and dedication of the authors to certain issues for which they have great interest.

To summarize, the book is an excellent description of the social structure, genealogy, and individual characteristics of killer whales that frequent the nearshore marine waters of British Columbia and Washington State. It does fall a bit short in some areas, but clearly it belongs in the collections of all marine mammal scientists and those amateur naturalists whose heads are turned by the alluring qualities of killer whales.

—Glenn R. VanBlaricom
Washington Cooperative Fish and
Wildlife Research Unit
School of Fisheries, WH-10
University of Washington
Seattle, Washington 98195

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Northwest Science

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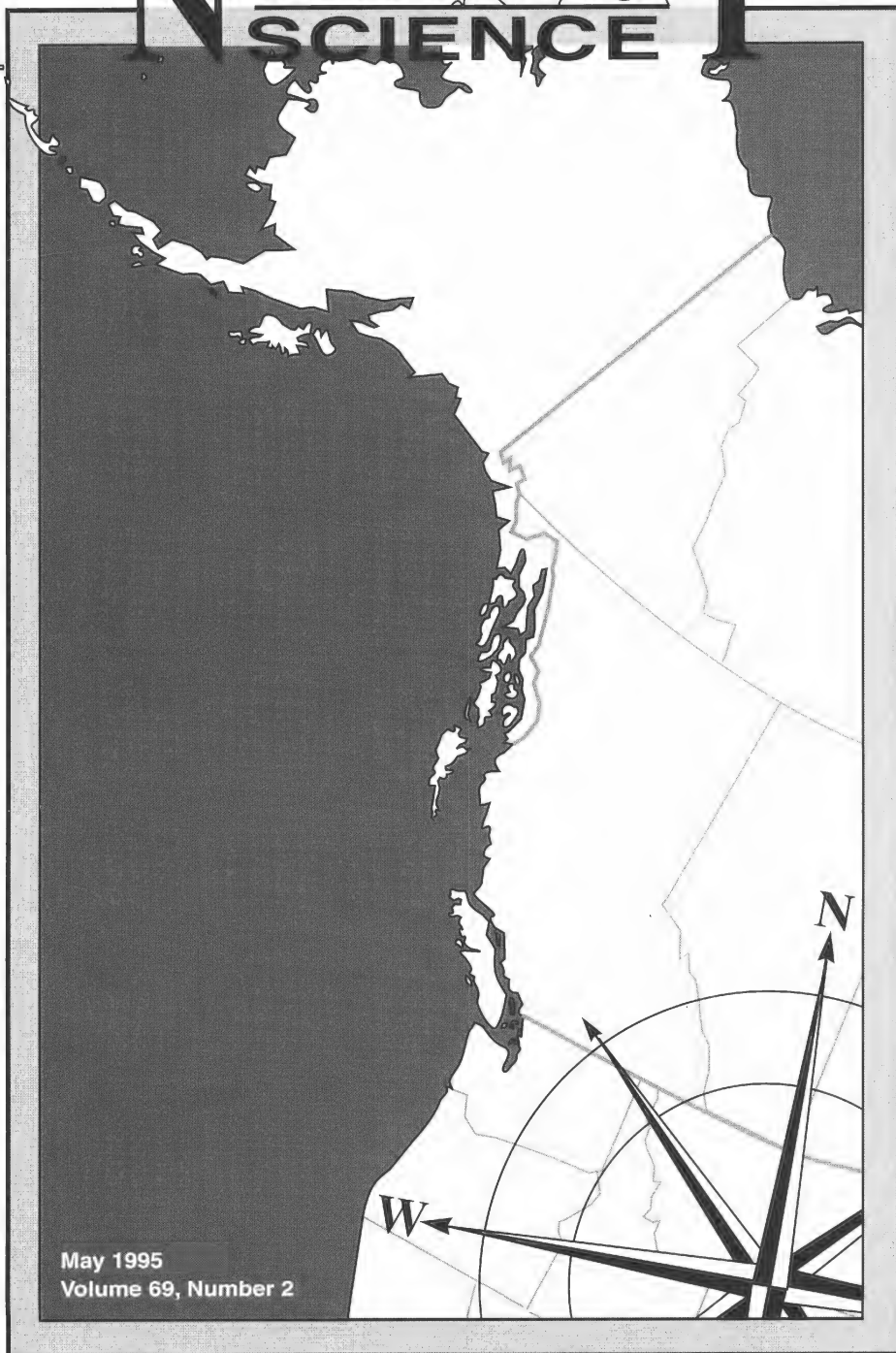
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Editor of *Northwest Science*

David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, Box 352100
Seattle, Washington 98195
Telephone: 206-543-1587
Fax: 206-685-0790
Internet: wild@u.washington.edu

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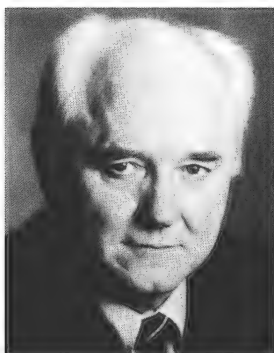
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Summary of Minutes of the Board Meeting of the Northwest Scientific Association, March 8, 1995

Announcements



Dr. Jack Ward Thomas Outstanding Scientist Award for 1995

Jack Ward Thomas is one of the best known and most widely recognized scientists in the Pacific Northwest. His career has focused on the biology and ecology of wildlife species, mainly in Oregon and Washington. His contributions have spanned the range from published field studies, to education and the incorporation of scientific thought into regional and national policy and land management actions. It is both the depth of scientific research and the wide range of influence that makes Dr. Thomas an outstanding scientist.

The major part of Dr. Thomas's research career has been spent in eastern Oregon, primarily studying elk, deer and turkey, wildlife diseases, wildlife habitat, songbird ecology and land-use planning. He has contributed approximately 300 technical publications in these fields. In addition, he has given approximately 275 technical presentations to symposia and technical meetings and an additional 74 to academic audiences such as the Starker Lectureship at Oregon State University. He has been associate editor or on the editorial board of several professional journals including the *Journal of Forestry* and *Forest Science*. He has held academic appointments at six universities. He has numerous other awards for service and publications, including outstanding publication of the year for "Elk of North America."

Jack Ward Thomas is best known for his work on the policies and land management actions revolving around the northern spotted owl in northern California, Oregon and Washington, where it is a federally listed Threatened Species. He is known as one of the principal architects of the Conservation Strategy for the northern spotted owl. He was team leader for the Scientific Analysis Team (SAT) and the Forest Ecosystem Analysis and Management Team (FEMAT), which led to the implementation of the President's Forest Plan in Washington, Oregon and California. He helped implement a paradigm shift from a single species management approach to more of an ecosystem management philosophy. He is currently Chief of the US Forest Service, where he leads and directs one of the country's largest land management agencies.

The Northwest Scientific Association is pleased to honor and recognize Dr. Jack Ward Thomas as its Outstanding Scientist for 1995.

1995 Student Research Grants

Each year the Northwest Scientific Association conducts an annual student research proposal competition. Small monetary awards are provided to support student research projects at colleges throughout the Northwest. Funds from this activity come from member contributions to the Association's research fund.

Four winners were announced at the 1995 meeting of the Northwest Scientific Association in Idaho Falls, Idaho. The winners and their research topics are:

- *John E. Banks*, University of Washington—The effect of landscape heterogeneity on pollinator movement: a study of patchiness and scale (\$400)
- *Julie Kaltenecker*, Boise State University—Post-fire recovery of microbiotic soil crusts on the western Snake River Plain (\$400)
- *Jeanne M. Ponzetti*, Oregon State University—Effects of grazing on biotic soil crust composition and cover in high desert ecosystems of the Pacific Northwest (\$400)
- *Jill Shellenberger*, Western Washington University—Antibacterial activity of Bryozoans in North Puget Sound (\$400)

The Pacific Northwest Regional Context Of The Climate of the H. J. Andrews Experimental Forest

Abstract

The H.J. Andrews (HJA) Experimental Forest, Oregon, Long-Term Ecological Research (LTER) site is a key research location in the Pacific Northwest (PNW). This paper endeavors to place the climate of the HJA into its regional context. Multiple regression analysis is used to create a synthetic record of monthly total precipitation (back to 1911) and monthly mean temperature (back to 1890). The observed (1973-1991) and synthetic (1911-1972) record is analyzed. Major features in the record are compared to the findings of other investigators particularly with respect to drought occurrence, recent warming, step functions and the tree ring record. The regional context of the HJA is addressed by relating its climate record to nearby climate divisional records and zonal and meridional indices of the general circulation of the atmosphere as well as commonly used teleconnective indices. GCM-related indices are found to be quite well related to the HJA climate record in winter but not in summer. Since most vegetative growth takes place in the spring and summer months, the ecological implications of this should be noted. There are quite strong relationships between the HJA winter water year precipitation and annual and January mean temperatures and the values of synoptic (regional) scale indices. No relationships are found for July. The Central North Pacific (CNP) index is a particularly well correlated with January and annual temperatures at the HJA. This is indicative of the importance of the magnitude and position of the Aleutian low pressure cell to the HJA temperatures. There is a weak but definite signal between the Southern Oscillation (SOI) index and the climate of the HJA such that during many warm events (El Niño years) the winter water year precipitation at the HJA Forest is relatively low and the annual mean temperatures are relatively high. During cold events (La Niña) the winter water year precipitation at the HJA Forest is relatively high, especially in the winter water year following a calendar year with a cold event, and the annual mean temperatures are relatively low. Overall, it is concluded that the climate of the HJA Forest is representative of the climate of the northern Cascades and their foothills in particular, and of the PNW in general.

Introduction

An enormous amount of basic and applied research has been performed at the H.J. Andrews (HJA) Experimental Forest, Oregon, Long-Term Ecological Research (LTER) site. Much of it has led to the development of current forest management policies. A number of projects are underway with the goal of scaling up findings at the HJA to a landscape or regional scale (Cohen *et al.*, 1992). It is important to establish how representative the site is of the Pacific Northwest (PNW) region. One way in which to approach the examination of representivity is to inquire how representative the climate of the site is compared to that of the PNW region as a whole? This paper seeks to investigate this question.

The H.J. Andrews Experimental Forest (HJA) is a 6400 ha forest of Douglas Fir, Western Hemlock, and Pacific Silver Fir located in the central portion of the western slope of the Cascade mountain range of Oregon. The forest is one of 18 sites in the Long-Term Ecological Research (LTER) program sponsored by the National Science Foundation (Franklin *et al.*, 1990). During the 1970s it was a representative site in the Coniferous Forest Biome Project of the U.S. International Biological Program. It was originally established in 1948 as

an Experimental Forest of the U.S. Forest Service. Consequently there is an immense legacy of research resulting from the participation in these research programs (McKee. *et al.*, 1987, Blinn *et al.*, 1988). Future LTER-related activities ensures the continuing scientific importance of the site.

A number of steps are taken in this paper in order to seek to answer the question of how representative is the climate of the HJA compared to that of the PNW as a whole? First the HJA climate will be briefly reviewed and an introduction is given to the aspects of the larger scale climate with particular emphasis on the importance of atmosphere-ocean interactions over the Pacific Ocean. Next, since the record of the HJA primary meteorological station is rather short, it is necessary to extrapolate it back in time and create a synthetic record. The observed (1973-1991) and synthetic (1911-1972) record is analyzed to identify some of its major features. These features are compared to the findings of other investigators particularly with respect to drought occurrence, recent warming, step functions and the tree ring record. The regional context of the HJA is then addressed by relating its climate record to nearby climate divisional records and zonal and meridional indices of the general circulation of the atmosphere as well as commonly used teleconnective indices.

Background Information

The Climate of HJA

Climatological information has been collected at the site since 1951 with a continuous, electronically sensed, record from May 1972. The observing system is composed of a primary meteorological station and a network of satellite temperature and precipitation recording stations. The primary meteorological station of HJA is at an elevation of 426 m (1397 ft) at latitude $44^{\circ} 15' N$ and longitude $122^{\circ} 10' W$. HJA occupies the Lookout Creek watershed which ranges from 420 to 1630 m (1378 to 5346 ft) and drains into the Blue River. Below 1050m (3444 ft), the Western Hemlock zone is found and is characterized by Western Hemlock and Douglas Fir. Above 1050m (3444 ft) the Pacific Silver Fir zone is established (Bierlmaier and McKee, 1989).

Bierlmaier and McKee (1989) have described the HJA climate as being wet and fairly mild in winter and warm and dry in summer. They emphasize the role of the polar front jet stream in funneling into the area one low pressure zone and frontal storm after another during the winter. Precipitation comes mainly from cold or occluded fronts. The storms are slowed by the Coast and Cascade ranges and are consequently of long duration and low intensity. The summer season is dominated by the establishment of a ridge of high pressure along the coast and the eastern Pacific. This season is characterized by highly stable air and low precipitation amounts. During the period 1973 to 1984 the average annual temperature was $8.5^{\circ} C$ ($47.3^{\circ} F$). Monthly temperatures ranged from $0.6^{\circ} C$ ($33.1^{\circ} F$) in January to $17.8^{\circ} C$ ($64.0^{\circ} F$) in July. The annual average precipitation was 2302 mm (90.6 ins) 71% of which fell from November through March. At 1203 m (3946 ft) annual precipitation rises to 2785 mm (109.7 ins). Above 1050 m (3444 ft) a persistent snow-pack up to 4 m (13 ft) deep may form and last into June (Bierlmaier and McKee, 1989). Further details of the climatology of HJA may be found in Emmingham and Lundburg (1977—quoted by (Bierlmaier and McKee, 1989)), Waring *et al.* (1978), and McKee and Bierlmaier (1987).

The regional climate of Oregon and the PNW and the importance of the Pacific Ocean Regional climatologies of the Oregon and the Pacific Northwest (PNW) have been given by Phillips (1960), Sternes (1960), the PNW River Basins Commis-

sion (1969) and Loy *et al.*, (1976). No understanding of the climate of the PNW would be complete without reference to the seminal role played by interactions between the ocean and atmosphere in the area of the northern Pacific Ocean and, to some degree, the tropical and southern parts of the Pacific as well. Namias pioneered this concept in a long series of important papers (1959, 1968, 1969, 1971, 1972, 1978, 1979, 1981). More recently the ocean-atmosphere interconnections have been treated in synoptic climatology through the use of principal component analysis (PCA) (Walsh and Richman, 1981) and teleconnections and in dynamic climatology increasingly by the use of General Circulation Models (GCMs) of the atmosphere and ocean.

The GCMs, by definition, deal with the atmosphere at the global scale. PCA and teleconnective studies, on the other hand, can be designed to investigate particular parts of the world and those studies relevant for the PNW are based on the Southern Oscillation Index (SOI), the Pacific-North American Index (PNA) and the Central North Pacific Index (CNP). These three indices exhibit a certain degree of intercorrelation (Cayan and Peterson, 1989). It should also be remembered that the strength of the teleconnective patterns is not necessarily stable over time. Ropelewski and Halpert (1986) have shown that depending on the data used, the PNW is either in, or is on the southern edge of, an area having lower rainfalls when El Niños are in progress and in many of the months following the El Niño maximum. Wallace and Gutzler (1981) were the first to introduce the PNA index. However, the PNA index designed by Leathers *et al.* (1991) following Yarnal and Diaz (1986) is the one used in this study. The PNA describes the amplitude of the 700 mb flow pattern over the U.S. which has a basic pattern of troughs of low pressure in the eastern Pacific and the eastern U.S., and a ridge of high pressure over the Rocky Mountain cordillera. The meridional extreme of the pattern produces positive PNA values (and potentially more SW winds over the HJA) while the zonal extreme produces negative PNA values (and potentially more W winds over the HJA). Yarnal and Diaz (1986) demonstrated how strongly positive PNA and negative (reverse) PNA patterns are associated respectively with warm and cold El Niño Southern Oscillation (ENSO) events and, in turn, with precipitation and temperature anomalies on the west coast of North America.

Cayan and Peterson (1989) designed the CNP index as being the mean sea level pressure (MSLP) over the region 35-55° N and 170° E to 150° W. They show that streamflow in the West have correlations in the range 0.3 to 0.6 SLP with anomalies in the North Pacific. During times of a weak CNP streamflows are high in Washington and Oregon. During times of a strong CNP the polar front jet stream flows north of the PNW and times of below average streamflow are observed. This is also often observed during El Niño events (See Cayan and Peterson, 1989, Figure 9). All of the synoptic studies indicate quite clearly the linkages which exist between SSTs and particular pressure and teleconnective patterns in the Pacific Ocean and various aspects of climate on the West Coast and the in the PNW.

Compilation of the Synthetic Record

It was first necessary to extrapolate the HJA climate record backwards in time. The stations most likely to give information for extrapolation were selected as being Corvallis, Cottage Grove, Eugene, Leaburg, McKenzie Bridge, and Cascadia. The station history of each of these was scrutinized for continuity using information for Oregon from Redmond (1985). Following analysis of pre and post move observations it was decided not to use the Eugene record. Multiple regression analysis was used to find the monthly values of mean temperature and total precipitation at the HJA from values at the stations which had been selected resulting from these screening procedures.

Precipitation

Precipitation data for the HJA site was obtained from five stations; Corvallis, Leaburg, McKenzie Bridge, Cascadia, and Cottage Grove. The multiple regression analysis identified good correlation in monthly and annual precipitation values between the stations. All regression equations were significant at the 99% level as assessed by their F values. Regression equations were computed for different sets of stations for three separate time periods which were determined by the length of record of the stations. The time periods were 1936-1972, 1919-1935, and 1910-1918. Table 1 shows the monthly range of r^2 and standard error of estimate (SEE) values for these time periods. The sum of the 12 monthly totals is used for the annual total value.

TABLE 1. Stations used, range of regression coefficients and standard error of estimates (mm) for multiple regression equations used to obtain monthly total precipitation at the H. J. Andrews Experimental Forest. Co is Corvallis, L is Leaburg, M is McKenzie Bridge, Ca is Cascadia, CG is Cottage Grove. All r^2 values significant at 99% level.

1936-1972 Co,L,M,Ca,CG			
Monthly r^2	0.89 to 0.98	SEE	7.6 to 46.0
Annual r^2	0.93	SEE	124.7
WatYr r^2	0.98	SEE	81.8
1919-1935 Co,Ca,CG			
Monthly r^2	0.83 to 0.94	SEE	8.4 to 53.9
Annual r^2	0.91	SEE	134.1
WatYr r^2	0.96	SEE	95.5
1910-1918 Co			
Monthly r^2	0.47 to 0.86	SEE	10.9 to 87.4
Annual r^2	0.61	SEE	255.3
WatYr r^2	0.77	SEE	214.1

A similar analysis was performed for precipitation values in the form of water year data. Following Johnson and Dart (1982) the water year is defined as the period October 1 to the next September 30 and the year is numbered for the year which includes the 9 month period. So the 1940 water year runs from October 1, 1939 to September 30, 1940. The analysis was also performed for the winter part of the water year (October to April). The selection of seasons this way follows the approach of Johnson and Dart (1982) and has obvious practical and hydrological advantages. As might be expected the water year and winter water year correlations carry a higher degree of accuracy than those for the calendar year. The values found in the present report are of the same order and are consistent with the findings of Johnson and Dart (1982 pp. 104-111) who worked on the whole state of Oregon.

Temperature

The same five predictor stations employed for estimating precipitation values were investigated using their average annual data between 1973 and 1991 for their efficiency in simulating temperature values. Correlation coefficient, SEE, and significance values between the five stations and the

TABLE 2. Stations used, range of regression coefficients and standard error of estimates ($^{\circ}\text{C}$) for multiple regression equations used to obtain mean monthly temperature at the H. J. Andrews Experimental Forest. Co is Corvallis, L is Leaburg, M is McKenzie Bridge, CG is Cottage Grove. All r^2 values significant at 99% level except where noted.

1936-1972 Co,L,M,CG		
Monthly r^2	0.69 to 0.92	SEE 0.47 to 1.02
Annual r^2	0.50 (95.0%)	SEE 0.57
1917-1935 Co,CG		
Monthly r^2	0.57 to 0.84	SEE 0.41 to 1.00
Annual r^2	0.49	SEE 0.53
1890-1916 Co		
Monthly r^2	0.56 to 0.84	SEE 0.59 to 1.09
Annual r^2	0.49	SEE 0.52

Andrews data indicated that the data from Cascadia had a detrimental effect on the strength of the regression equations. Cascadia was therefore omitted for the rest of the analysis. The range of individual monthly regressions (Table 2) displays slightly lower correlations than for precipitation but still shows strong values.

Simulated monthly mean temperature and total precipitation data verified well against an actual observed independent data set for the period 1951 to 1972 from Watershed #2 in the HJA Forest. It was concluded that the simulated temperature and precipitation series have an accuracy level which certainly justifies further temporal and spatial analysis of the data.

Analysis Of The Synthetic And Observed Record

Precipitation

The total water year precipitation record from 1911 to 1991 displays considerable interannual variability (Figure 1). The trends represented by the five year running mean of the same data plainly show the prolonged and severe drought of the 1930s and the wetter years of the late 1940s and the 1950s (Figure 2). The record exhibits greater variability in more recent years with two peaks of precipitation centered on 1973 and 1984 with droughts centered on the late 1970s and one which persisted through, at least, 1991. In the case of both the most recent drought and that of the 1970s, as judged by the value of water year precipitation, both were as severe as the drought of the 1930s

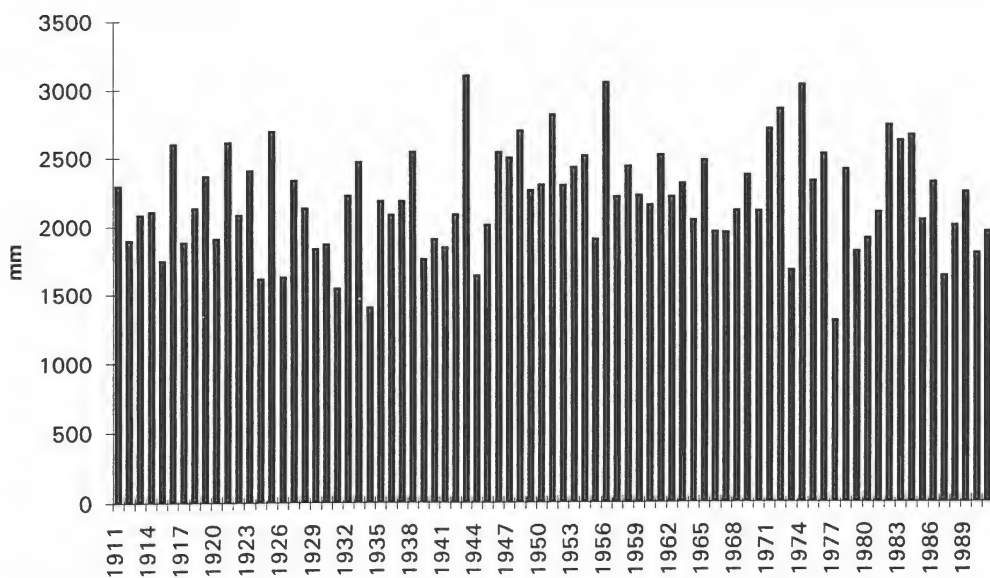


Figure 1. Total annual precipitation by water year at the H.J. Andrews Experimental Forest Primary Meteorological Site 1911-1991. Values prior to 1973 are obtained by regression analysis.

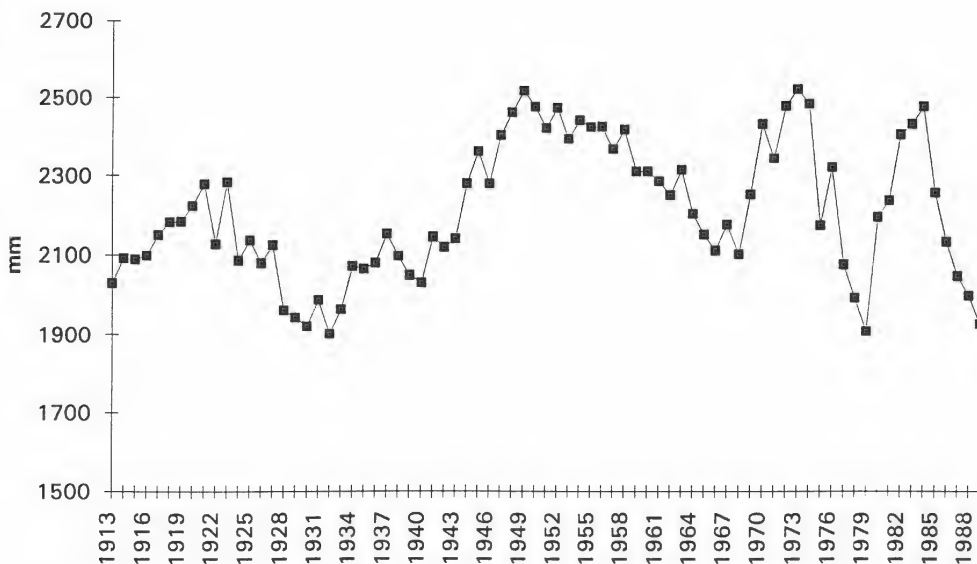


Figure 2. Five year running mean of water year total precipitation at the H.J. Andrews Experimental Forest Primary Meteorological Site 1911-1991. Values prior to 1973 are obtained by regression analysis.

but at least the 1970s drought did not last so long. The variations of precipitation at the HJA found here match quite well trends in the Willamette Valley described by Johnson and Dart (1982). Johnson and Dart also note high interannual variability and correspondingly, relatively few groupings of wet or dry years for western Oregon.

Temperature

The observed and synthetic annual mean temperature record for the HJA from 1890-1991 also shows considerable interannual variability (Figure 3). Five year running means exhibit a warming trend between the beginning of the record and the early 1940s punctuated by two cool periods in the early 1910s and the early 1920s respectively (Figure 4). A cool period is seen from the late 1940s to the mid 1970s with the exception of one warm year (1958). Finally, a warming trend is seen from the mid 1970s to the present time. However, the magnitude of this trend, at least up to 1991, is similar to that of the warming trend at the beginning of the century.

Bradley (1982) notes that 1921-35 stand out over the Western U.S. as anomalously warm in the context of the last 100 years. The HJA data do

show high temperatures during this time. 8 of the 15 years of this period at HJA have above (1890-1991) mean temperatures with 3 of the years exceeding the mean by 1 standard deviation (SD). A comparison of individual years of high and low temperatures for Oregon as a whole identified by Bradley is not easily possible in the absence of Bradley's data in a tabular form. A comparison of low and high temperature winters for selected West Coast stations (Roden, 1989) shows that more often than not the HJA values parallel the coastal values.

Recent Warming

Since there has been considerable evidence of a trend for minimum temperatures to increase over the last two to three decades (Karl *et al.* 1988), the observed HJA record was examined to see if it contained this signal. Maximum, minimum, and mean seasonal and annual temperatures were regressed against year number for the period 1973-1991. The period at the HJA had not only increasing minimum temperatures but increasing maximum and mean temperatures as well. The fact that the greatest increases occurred in the spring (March, April, May) possibly affecting growth rates

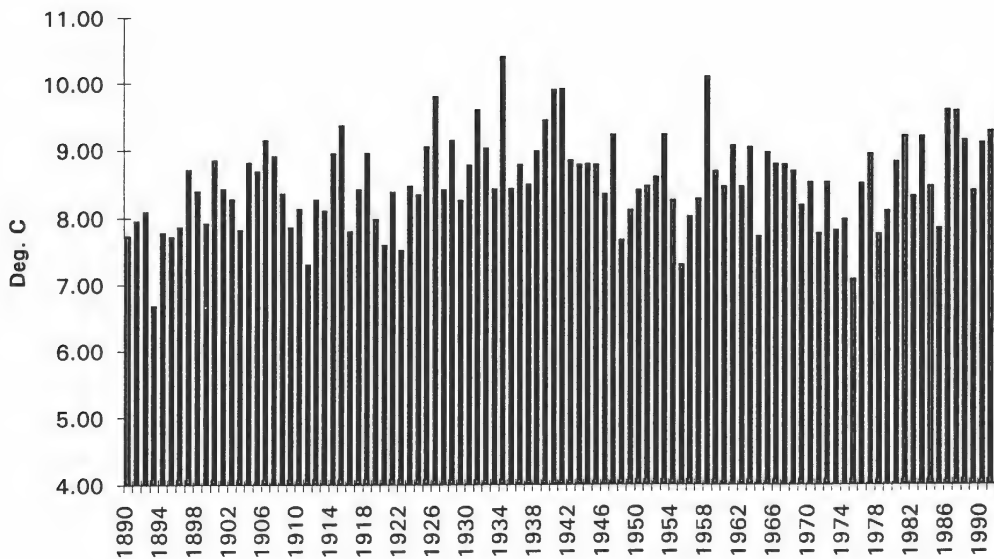


Figure 3. Mean annual temperature at the H.J. Andrews Experimental Forest Primary Meteorological Site 1890-1991. Values prior to 1973 are obtained by regression analysis.

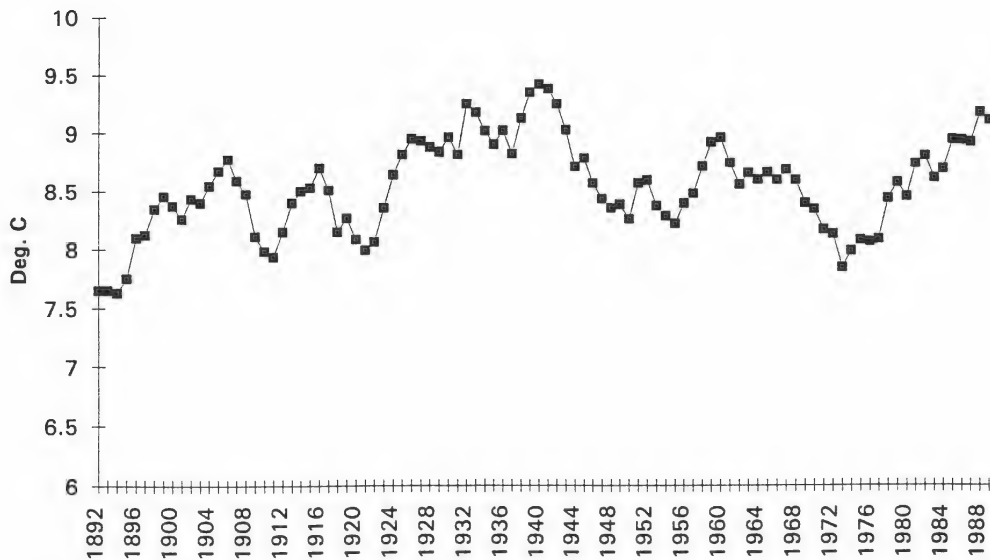


Figure 4. Five year running mean of mean annual temperature at the H.J. Andrews Experimental Forest Primary Meteorological Site 1890-1991. Values prior to 1973 are obtained by regression analysis.

at this time is of ecological importance. The warming is also seen at Corvallis and Cottage Grove although in not quite as an intense form and not during the winter season. It is important to reiterate that the magnitude of this recent warming trend is similar to one that took place at HJA at the beginning of the century.

Step Functions

Several investigators have identified step functions in certain of the meteorological time series during the period of the modern record. Ebbesmeyer *et al.* (1991) have investigated a step function occurring in biogeophysical time series of the PNW and the Pacific in 1976. Leathers and Palecki (1992) have identified a step function occurring in the value of the PNA index during the late 1950s and centered approximately on 1957. The 1957 step was also noticed in records of the mean height of sea level along the West Coast (Namias, 1972). An analysis was performed to investigate whether such steps exist in the climatic data for the HJA Forest.

First the difference of the means before and after the steps were tested using a two-tailed *t* test. Using the means of the 8 years before and after the 1976 step there was a significant difference (99% level) in the HJA Forest annual mean temperatures. A significant difference (99% level) was also displayed in annual mean temperatures when 15 year means either side of 1976 were taken. No significant difference was seen in the winter water year precipitation values at the HJA Forest when 8 year means were taken either side of 1976 but a significant difference (95% level) was found in these values when a 15 year mean either side of 1976 was selected.

No significant differences were found in HJA Forest annual mean temperatures or winter water year precipitations between 18 year means or 8 year means either side of 1957. At first this result seems hard to explain since there is a weak relationship between the PNA values and HJA precipitation and temperature values (Tables 5 and 6). However, this relationship is seen more in winter values rather than annual values. Perhaps more important is the fact that Leathers and Palecki (1992) show that the 1957 PNA step is seen most clearly in the S.E. United States center of action of the PNA index rather than either of the two centers closer to the PNW.

Thus it may be concluded that there is evidence in the HJA Forest record for the 1976 step but not for the PNA-related 1957 step. However we interpret the Andrews record in terms of pre and post 1976 values, it is clear that the year 1976 was a marked turning point at the HJA for both temperature and precipitation. For approximately 15 years prior to 1976 the annual temperature trend had been downward. Since that time the annual temperature trend has been upwards. In absolute terms the 1977 water year (which includes the winter of 1976-77) had the lowest precipitation values in the entire record with generally higher values both before 1977 and after it. The five year running mean of these data places the turning point two years later. Clearly the atmosphere changed to a different mode of operation in the mid 1970s and this change is well represented in the HJA data as well as that of many other parts of the PNW.

The Tree Ring Record

The general temporal variation which Graumlich (1987) reports in a study of tree ring width data for the present century in her defined Western Lowlands and Columbia Basin (but not the Southern Valleys) divisions is similar to the HJA precipitation record. Data from HJA are generally consistent with those of Graumlich and tend to suggest that her findings for earlier years back to 1640 would also be applicable to the Andrews. More confidence should be attributed to runs of dry, and presumably wet, years rather than for individual years. One reason for this is the masking of extreme values in the simulated HJA data which is related to the least squares analysis methodology. Graumlich finds marked droughts occurring in the Columbia Basin around 1680, and in the 1750s, 1780s, 1790s, 1840s, 1865-1895, and in the 1920s and 1930s. Wet periods occurred from 1695-1715, 1740-1760, and 1810-1835. Examination of Graumlich's graphical data indicates that in the 1750s there were individual years of both extreme wetness and drought. The wet and dry periods were similar in the Western Lowlands except that the duration of droughts was less. Hatton (1989) found similar results from a tree ring record at Lost Forest located in the eastern end of the Fort Rock Basin in Lake County in central Oregon.

Graumlich and Brubaker (1986) analyzed a tree ring record for Longmire, Washington, and

commented that the temperatures between 1900 and 1940 were higher than any other extended 40 year period. HJA temperature data for the present century also display high temperatures during this time and thus give rise to the implication that earlier "warm" periods found in the Washington record also occur at the HJA Forest. These warm periods occurred between 1655-1670, 1690-1695, and 1825-1830. "Cool" periods in the Longmire record occurred between 1610-1630, 1640-1650, 1695-1760, 1800-1808, 1840-1850, and 1875-1895.

The Regional Context

Climate Divisional Data

The synthetic and observed precipitation data for the HJA site for the period 1915 to 1991 were compared by correlation techniques on a month by month and annual basis with precipitation data from the Willamette Valley (OR2) and the Northern Cascades (OR4) Oregon Climate Divisions. There exists a slight degree of autocorrelation since data from some of the stations in the divisions were used to simulate part of the HJA data set. However, the autocorrelation is very small as Cascadia, Corvallis, Cottage Grove, and Leaburg are just 4 of the 33 stations in the Willamette Valley Division and McKenzie Bridge is just one of eight stations in the Northern Cascades Divisions. Consequently it is reasonable to assume that the small amount of autocorrelation does not markedly affect the results from this analysis.

For precipitation, the relevant r^2 values indicate a strong relation between the HJA site and both the Willamette Valley and the Northern Cascades divisional data. Monthly correlation coefficient values range from 0.60 to 0.92. It is remarkable that high values are found even for the summer months. On the basis of these values the precipitation at the Andrews is slightly more related to the Northern Cascades division (in which it is located) but the high r^2 values indicate it is representative of the area covered by both divisions. The monthly correlation coefficients between the temperature values of the climatic divisions and the HJA Forest are slightly lower than those for precipitation and range from 0.59 to 0.87. The Willamette Valley division has the higher correlation values in most cases. This may be due to the high degree of variation of temperature values in complex terrain associated with the wide variety of different microclimates.

General Circulation Indices

The observed and synthetic HJA data were compared with general circulation indices designed to relate to the PNW region following an approach of Wigley *et al.* (1990) and Jones (1991) who were interested in the question of how to estimate regional values of projected climate change from the projected values at grid points on the coarse network of points used by current GCMs. The indices were constructed for use with a data set of reconstructed monthly MSLP developed by Jones *et al.* (1987). The data for North America is on a 5° latitude by 10° longitude grid. Following the approach by Jones (1991) three general circulation indices were developed. The first was simply a pressure index, (SLP) at $45^\circ\text{N } 120^\circ\text{W}$, a location which happens to be in the center of Oregon and not far from the HJA. The second was a zonal index comprised of the difference in SLP between $40^\circ\text{N } 120^\circ\text{W}$ and $50^\circ\text{N } 120^\circ\text{W}$. Positive values of this index indicate the general strength of westerly winds. The third index was a meridional index comprised of the difference in SLP between $45^\circ\text{N } 120^\circ\text{W}$ and $45^\circ\text{N } 130^\circ\text{W}$. Positive values of this index indicate the general strength of southerly winds. These points differ somewhat from those employed in Jones' original study. In order to clarify the regression analysis, the value of the first index was modified by subtracting 1014 mb from each value.

The correlation coefficients for the temporally aggregated data (Table 3) indicate a slight correlation between the Central Oregon SLP and winter water year precipitation and between the meridional index and annual mean temperature, where southerly winds are expectedly associated with higher temperatures, but no other relationships are apparent. On the monthly time scale there is greater correlation of HJA temperature and precipitation values and the circulation indices in January but no correlation in July (Table 4). This is to be expected given the more vigorous general circulation in the Northern hemisphere winter and the low absolute amount of precipitation at the HJA in summer. In order to be more consistent with Jones' analysis, all three circulation indicators were used together in a multiple regression for January and July. This analysis yielded correlation coefficients of 0.56 (January temperature) and 0.52 (January precipitation) which is comparable to Jones' findings and 0.04 (July temperature) and 0.19 (July precipitation) which is much lower than

TABLE 3. Correlation coefficient values between annual mean temperature and winter water year precipitation totals at the HJA and selected general circulation indices.

Variable Regressed Against	r ²	Significance Level (%)
<i>Winter water year precipitation 1914-1980</i>		
Central Oregon Pressure	0.24	99
Zonal Index	0.15	99
Meridional Index	0.03	<95
<i>Annual mean temperature 1890-1980</i>		
Central Oregon Pressure	0.01	<95
Zonal Index	0.01	<95
Meridional Index	0.36	99

TABLE 4. Correlation coefficient values between January and July mean temperature and precipitation totals at the HJA and selected general circulation indices for the period 1914-1980.

Variable Regressed Against	Jan		July	
	r ²	Sig Level %	r ²	Sig Level %
<i>Precipitation</i>				
Central Oregon Pressure	0.29	99	0.03	<95
Zonal Index	0.22	99	0.04	<95
Meridional Index	0.07	95	0.04	<95
All three indices	0.52	99	0.19	99
<i>Temperature</i>				
Central Oregon Pressure	0.32	95	0.00	<95
Zonal Index	0.32	99	0.04	<95
Meridional Index	0.28	99	0.00	<95
All three indices	0.56	99	0.04	<95

Jones found for the general location of the HJA. In summary, the relationships in winter are much stronger than those in summer. The implication of these results is that output values predicted by GCMs for the general area of the PNW may be applied to the HJA with more confidence in the winter season than in summer. Most vegetative growth takes place in the spring and summer months therefore projections made from GCMs for the PNW for the growing season should be treated with some caution.

PNA and CNP Indices

Correlations were also made between the HJA data and the PNA and the CNP indices for the period 1948-87. The results (Figure 4. top, Figure 5. top, Tables 5 and 6), in the context of this kind of synoptic climatological analysis, indicate quite marked correlations between HJA winter water year precipitation and both indices. Precipitation at the HJA for January, representing the winter months, also displays a weak but significant correlation with both indices. No relationships are seen for July, representing the summer months, or for the

TABLE 5. Correlation coefficient values between Annual, January and July mean precipitation totals at the HJA and selected general circulation indices for the period 1948-1987.

Variable Regressed Against	r ²	Significance Level (%)
PNA Annual	0.08	<95
PNA Winter Water Year	0.25	99
PNA January	0.16	95
PNA July	0.00	<95
CNP Annual	0.04	<95
CNP Winter Water Year	0.17	99
CNP January	0.10	95
CNP July	0.06	<95
CNP Annual (1914-1990)	0.03	<95
CNP Winter Water Year (1914-1990)	0.21	99
CNP January (1914-1990)	0.11	99
CNP July (1914-1990)	0.03	<95

TABLE 6. Correlation coefficient values between Annual, January and July mean temperature at the HJA and selected general circulation indices for the period 1948-1987.

Variable Regressed Against	r ²	Significance Level (%)
PNA Annual	0.12	95
PNA January	0.40	99
PNA July	0.11	95
CNP Annual	0.45	99
CNP January	0.40	99
CNP July	0.04	<95
CNP Annual (1910-1990)	0.44	99
CNP January (1910-1990)	0.31	99
CNP July (1910-1990)	0.05	95

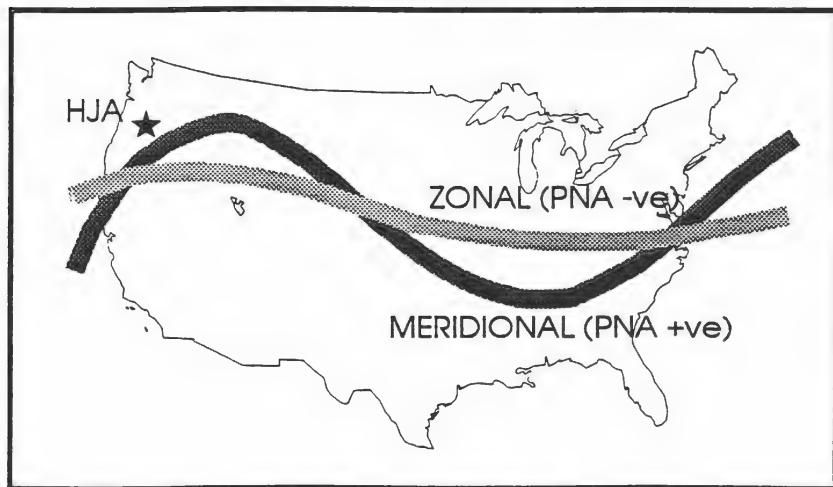
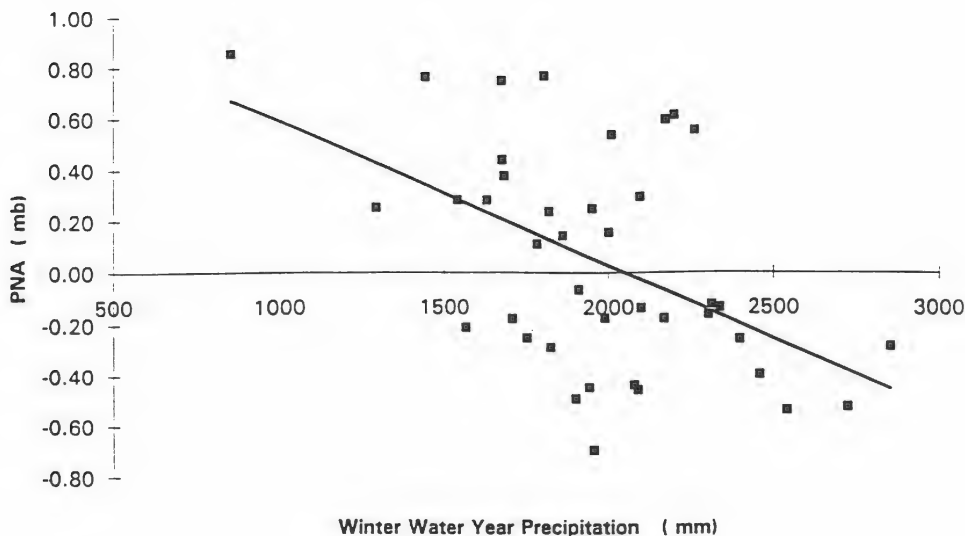


Figure 5. Top: The relationship between total winter water year (WWY) precipitation at the H.J. Andrews Experimental Forest and the PNA index value for the same period. Bottom: a conceptualization (following Leathers *et al.* 1991) of the character of the 700 mb westerly flow over the United States accompanying positive and negative values of the PNA index. When the PNA index is positive and high, a meridional circulation in the westerlies with a ridge of high pressure shunts storms to the north of Oregon (and the HJA) gives rise to relatively dry conditions.

calendar year totals of precipitation. Annual and January mean values of temperature exhibit a very strong correlation with the CNP index. The rela-

tionship of January mean temperatures to the PNA index is also very strong while the relationships for the year and for July are not so strong but are

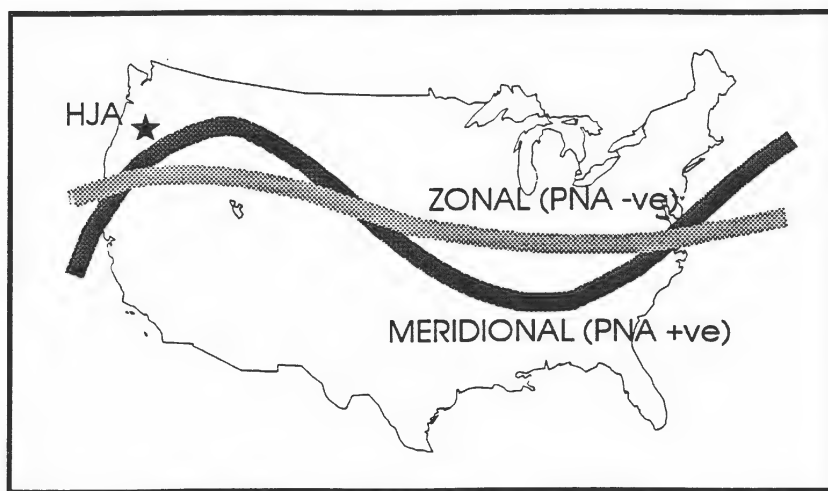
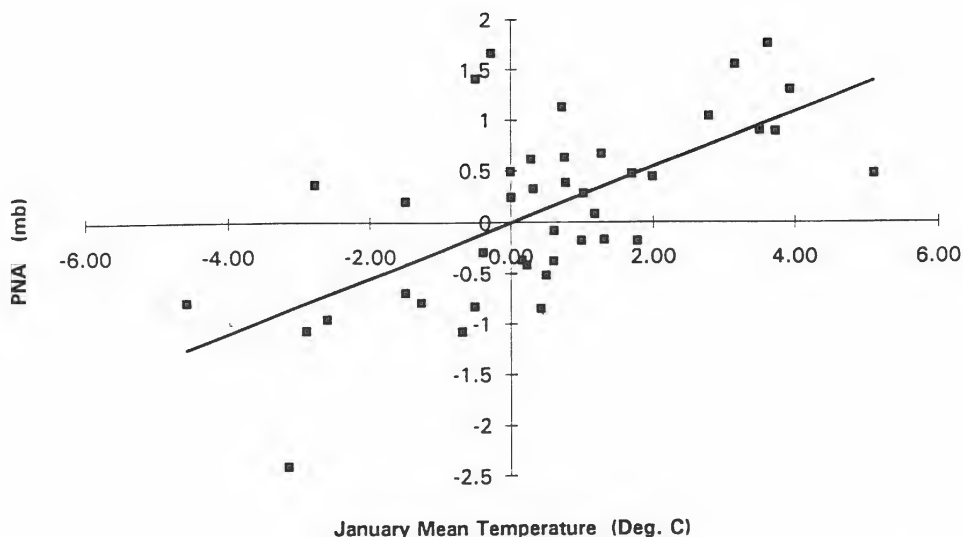


Figure 6. Top: The relationship between mean January temperature at the H.J. Andrews Experimental Forest and the PNA index value for the same period. Bottom: a conceptualization (following Leathers *et al.* 1991) of the character of the 700 mb westerly flow over the United States accompanying positive and negative values of the PNA index. When the PNA index is positive and high, a meridional circulation in the westerlies with a ridge of high pressure gives rise at the HJA to warm air from the southwest with relatively high temperatures.

significant. Redmond and Koch (1991) also found significant relationships between concurrent precipitation and temperature values in the PNW and PNA values with temperature having the strongest relationship.

Physically (Figs. 5 and 6 bottom), when the PNA index is positive and high, a meridional circulation in the westerlies with a ridge of high pressure shunts storms to the north of Oregon (and the HJA) giving rise to relatively dry weather. This

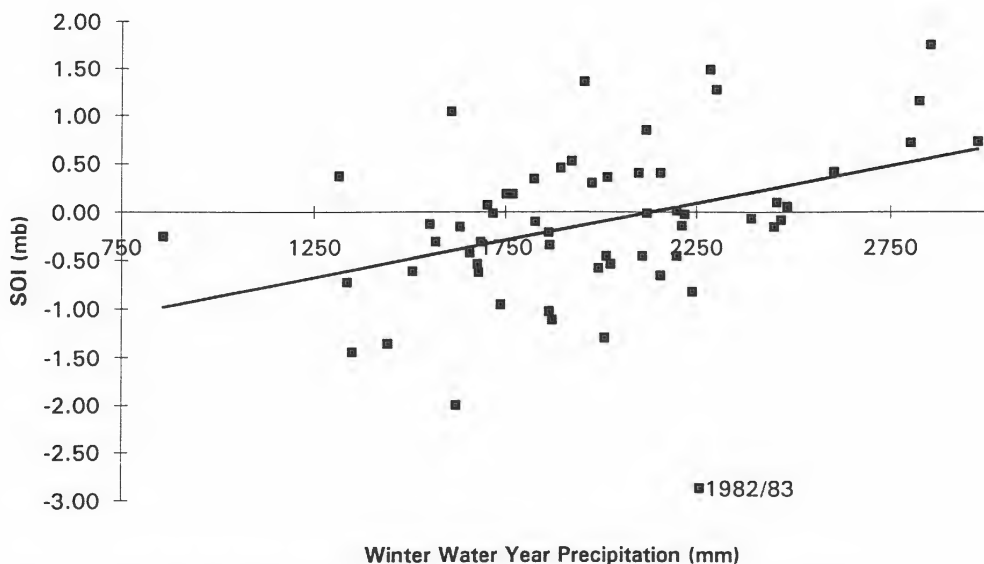


Figure 7. The relationship between winter water year (WWY) precipitation totals at the H.J. Andrews Experimental Forest and the values of the SOI index for the same period.

situation also brings in warm air from the southwest with relatively high temperatures. When the PNA index is negative, the zonal circulation in the westerlies brings in storms from the Pacific Ocean giving rise to wetter weather and rather lower air temperatures. These interpretations are also consistent with the CNP values which, when low, indicate that a well developed Aleutian low pressure zone will guide storms northwards to British Columbia but when high will allow storms to travel more directly eastwards into Washington and Oregon.

The advantage of using the CNP is that it has a long record dating back to 1899. Comparison of the relationships between HJA data and the CNP index for the longer periods of 1910 or 1914 to 1990 (Tables 5 and 6) indicates little difference in the correlation coefficients that were found for the shorter 1948-1990 period. This is encouraging because it suggests that the relationships are fairly stable over time and the time series are somewhat stationary.

SOI Index

Direct comparison of winter water year HJA values and SOI values suggests a relationship in which low SOI values (warm event, El Niño years) tend to be associated with low precipitation values at the

HJA and high SOI values (cold event, La Niña years) tend to be associated with high precipitation values at the HJA (Fig 7). The relationship is clear although it is not very strong statistically ($r^2=0.14$, significant at 99%). The 1983 year which had an extraordinary strong low SOI value is a noteworthy outlier on the scattergram. Without the 1983 value the relationship is stronger ($r^2=0.23$ significant at 99%). A similar, though stronger and reverse, relationship exists on an annual time scale between the SOI values and the annual mean temperature at the HJA Forest (with the inclusion of the 1983 data point $r^2=0.24$, significant at 99%) (Figure 8).

Further light is given to this issue by examining HJA climate values for extreme SOI years. Two sets of extreme SOI years have been provided respectively by Yarnal and Diaz (1986) and Halpert and Ropelewski (1992). Yarnal and Diaz identified a number of warm (El Niño) and cold (La Niña) event winters (Dec, Jan and Feb). During warm event winters, HJA precipitation is near average at 0.03 SD of the long term (1914-1991) mean and the temperature is well above (0.77 SD) the long term (1890-1991) mean. During cold event winters HJA precipitation is well above (0.69 SD) the long term mean and temperature is below it (-0.33 SD). Halpert and Ropelewski defined warm

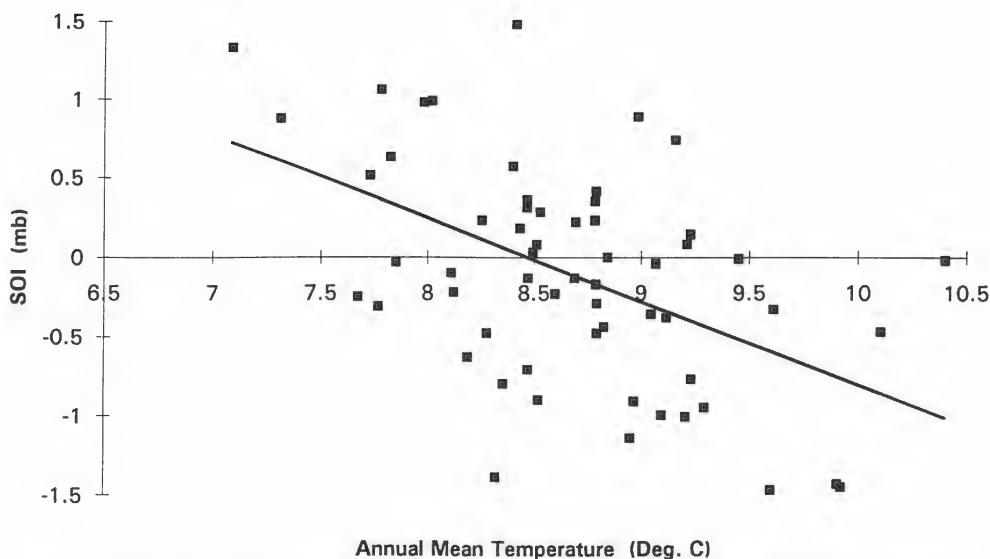


Figure 8. The relationship between annual mean temperature at the H.J. Andrews Experimental Forest and the values of the SOI index for the same period.

event years as those in which the SOI index value remained in the lower 25% of the distribution for 5 months or longer and similarly defined cold events years by using the upper 25% of the distribution. By these definitions, at the HJA during warm event years, the annual precipitation is near the long term mean (-0.02 SD), the winter water year precipitation is slightly above the long term mean (0.15 SD) but the following winter water year is markedly below the long term mean (-0.32 SD). Also during warm event years, HJA temperatures are well above the long term mean (0.45 SD). During cold event years HJA annual precipitation is well above the long term mean (0.48 SD) although the winter water year precipitation is near the long term mean (-0.05 SD). Most striking however is that during cold event years the following winter water year is 0.88 SD above the long term mean. Also during the cold event years the annual mean temperature is notably below (-0.37 SD) the long term mean.

Thus it seems there are definite relationships such that during many warm events (El Niño years) the winter water year precipitation at the HJA Forest is relatively low and the annual mean temperatures are relatively high. During cold events (La Niña years) the winter water year precipitation at the HJA Forest is relatively high, especially in the winter water year following a calendar year with

a cold event, and the annual mean temperatures are relatively low. These findings are consistent with those of Yarnal and Diaz (1986) and Redmond and Koch (1991). The latter noted for the PNW as a whole that precipitation is low and temperature is high during low SOI values with the opposite also being true. Interestingly they found that the relationship tended to be strongest in the mountainous climate divisions. They point out that a combination of low precipitation and high temperature values implies a smaller than average snowpack during El Niño years.

With one exception, there were no significant correlations in either precipitation or temperature when the data were lagged at monthly intervals. The exception was a weak relationship between HJA January precipitation and the SOI value of the previous March ($r^2 = 0.10$ significant at 95%). The relationship is interesting enough to pursue at a later time using seasonal as opposed to monthly data.

Conclusions

The most important findings of this study may be summarized as follows:

- 1) It is feasible to extend backwards in time, records of mean monthly precipitation and mean monthly temperature.

2) The synthetic record shows considerable interannual variability both in precipitation and in temperature.

3) The warming of approximately the last two decades is, so far, no greater than a similar warming which took place at the beginning of the century. The recent warming is found not only in minimum temperatures but also in maximum and mean temperatures. It is found in all seasons but is most marked in spring. For the most part it is paralleled by, but is greater than, the warming at Corvallis and Cottage Grove.

4) The drought of the late 1980s and early 1990s was similar in magnitude to that of the mid 1970s and similar in magnitude but not, so far, duration of that to the 1930s.

5) Both the precipitation and the temperature record at the HJA are in general agreement with what is known from other studies of temporal changes in Oregon and the PNW.

6) The HJA record agrees in general with the tree ring record of the larger scale region.

7) There is evidence that a step function at 1976 which has been found in other biophysical time series in the PNW also occurs in HJA precipitation and temperature values. There was no evidence found in these values for a step function centered on 1957.

8) The climate record of the HJA is closely related to that of the Willamette Valley and Northern Cascades climatic divisions of Oregon.

9) Local GCM-related indices are quite well related to the HJA climate record in winter but not in summer. Hence, we can have some confidence that whatever climatic change is projected by GCMs for the PNW will be applicable in large measure to the HJA Forest in winter and for the winter water year. The implication of these results is that output values predicted by GCMs for the general area of the PNW may be applied to the HJA with more confidence in the winter season than in summer. However, most vegetative growth takes place in the spring and summer months therefore projections made from GCMs for the PNW for the growing season should be treated with some caution.

10) By the standards usually applied in synoptic climatology there are quite strong relationships between the HJA winter water year precipitation and annual and January mean temperatures and both the PNA and the CNP indices. No relationships are found for July. The CNP index is a par-

ticularly well correlated with January and annual temperatures at the HJA. This is indicative of the importance of the magnitude and position of the Aleutian low pressure cell to the HJA temperatures.

11) There is a weak but definite signal between the SOI (ENSO) index and the climate of the HJA such that during many warm events (El Niño years) the winter water year precipitation at the HJA Forest is relatively low and the annual mean temperatures are relatively high. During cold events (La Niña) the winter water year precipitation at the HJA Forest is relatively high, especially in the winter water year following a calendar year with a cold event, and the annual mean temperatures are relatively low.

Researchers at most LTER sites, except those where long period records already exist, would benefit by having a climate record at their sites extended back into the last century. The foregoing discussions provide a model methodology for local climate analysis and synthesis at LTER sites. While synthesis by regression analysis is not new, the placement of the site into its regional context by using relations with Climatic Division data and local and hemispheric general circulation indices does provide a new method of viewing the local climatic environment. This methodology will become increasingly important as LTER sites begin to scale up to landscape and regional levels as is the case for the HJA. It should be noted that it cannot be assumed *a priori* that any single LTER site will relate well to the larger regional climatic environment. This has been demonstrated, for example, for the Niwot Ridge, Colorado, LTER site (Greenland and Swift, 1991).

The original question of how representative is the HJA climate of that of the PNW as a whole has largely been answered by the foregoing analyses. Comparisons of the HJA climate with values from nearby Climatic Divisions, and local and hemispheric general circulation indices all suggest that the climate of the HJA Forest is well representative of the climate of the northern Cascades and their foothills in particular and of the PNW in general. However as one moves to the larger geographic scale indices, the relationships become less strong and even non-existent in the summer months. The reason for this is that during these months the HJA is usually dominated by a ridge of high pressure and the processes of microclimatology tend to dominate those of larger scales. In contrast, in winter with the expansion of the high

energy circumpolar vortex into mid latitudes, and with our growing awareness of the linkages between tropical and extra-tropical circulations, it is not surprising that the HJA is well coupled with these hemispheric scale features. Although focused mainly on the winter months this coupling has important implications for the climate of the HJA one or two, or possibly more, seasons ahead and thus allowing a new dimension in planning ecological experiments.

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Literature Cited

- Blinn, T., F. J. Swanson, and A. McKee. 1988. Research Publications of the H.J. Andrews Experimental Forest, Cascade Range, Oregon, 1988 Supplement. General Technical Report, PNW-GWT-223. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 26 p.
- Bierlmaier, F. A., and A. McKee. 1989. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972-1984. USDA Forest Service, Pacific Northwest Research Station. Portland, OR. General Technical Report. PNW-GTR-223 26 pp.
- Bradley, R. S. 1982. Climatic fluctuations of the western United States during the period of instrumental records. Ch. 1 (pp. 1-76) in *Climatic fluctuations of the western United States during the period of instrumental records*, by Bradley, R.S., Barry, R.G., and Kiladis, G. Contribution No. 42. Department of Geology and Geography, University of Massachusetts. Amherst, Mass. 01003-0026. 169 pp.
- Cayan, D. R., and D. H. Peterson. 1989. The Influence of North Pacific Circulation on Streamflow in the West. in: *Aspects of climate variability in the Pacific and western Americas*. Ed. D. H. Peterson. American Geophysical Union. 445 pp. pp. 375-397.
- Cohen, W. B., D. O. Wallin, M. E. Harmon, P. Sollins, C. Daly and W.K. Ferrell. 1992. Modeling the effect of land use on carbon storage in the forests of the Pacific Northwest. pp. 1023-1026 in *Proceedings of the International Geosciences and Remote Sensing Symposium*, IEEE catalog #92CH3041-1.
- Ebbesmeyer, C.C., D. R. Cayan, D. R. McLain, F. H. Nichols, D. H. Peterson, and K. T. Redmond. 1991. 1976 Step in the Pacific Climate: Forty Environmental Changes between 1968-1975 and 1977-1984. in: J. L. Betancourt and V. L. Tharp, Eds, *Proceedings of the Seventh Annual Pacific Climate (PACIM) Workshop*, April 1990. California Department of Water Resources, Interagency Ecological Studies Program. Technical Report 26. pp. 115-126.
- Franklin, J. F., C. S. Bledsoe, and J. T. Callahan. 1990. Contributions of the Long-Term Ecological Research Program. *Bioscience*. 40(7):509-523.
- Graumlich, L. J. 1987. Precipitation variation in the Pacific Northwest (1675-1975) as reconstructed from tree rings. *Annals of the Association of American Geographers*. 77(1):19-29.
- Graumlich, L. J. and L. Brubaker. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, Washington, derived from tree rings. *Quaternary Research*. 25:223-234.
- Greenland, D. and L. W. Swift, Jr. 1991. Climate variability and ecosystem response: opportunities for the LTER network. *Bulletin of the Ecological Society of America*. 72(2):118-126.
- Halpert, M. S. and C. F. Ropelewski. 1992. Surface temperature patterns associated with the Southern Oscillation. *Journal of Climate*. 5:577-593.
- Hatton, R. R. 1989. Climatic variations and agricultural settlement in southeastern Oregon. Ph.D. Dissertation. Department of Geography. University of Oregon. 1989. 262 pp.
- Johnson, D. M. and J. O. Dart. 1982. Variability of precipitation in the Pacific Northwest: Spatial and Temporal Characteristics. Water Resources Research Institute, Oregon State University. Corvallis, OR. WRRRI-77. 181 pp.
- Jones, P. D. 1991. How much of the local climate variability can be explained by large-scale changes? *Proceedings of the 20th Conference on Agricultural and Forest Meteorology*, Sept. 10-13, 1991, Salt Lake City, Utah. American Meteorological Society. Boston MA. pp J7-J14.
- Jones P. D., T. M. L. Wigley, and K. R. Briffa. 1987. Monthly Mean Pressure Reconstructions for Europe (Back to 1780) and North America (to 1858). U.S. Dept. of Energy. Report DOE/ER/60397-H1. 99 pp.
- Karl, T. R., R. G. Baldwin, M. G. Burgin. 1988. Historical Climatology Series. 4-5. National Climatic Data Center. 107 pp.

- Leathers, D. J., B. Yarnal, and M. A. Palecki. 1991. The Pacific/North American teleconnection pattern and United States climate. Part I: Regional temperature and precipitation associations. *Journal of Climate*. 4(5):517-528.
- Leathers, D. J. and M. A. Palecki. 1992. The Pacific/North American teleconnection pattern and the United States climate. Part II: Temporal Characteristics and index specification. *Journal of Climate*. 5:707-716.
- Loy, W. G., S. Allan, and C. P. Patton. 1976. *Atlas of Oregon*. University of Oregon Press. Eugene. 215 pp.
- McKee, A. and F. Bierlmaier. 1987. H.J. Andrews Experimental Forest, Oregon. Ch.2. In *The climates of the Long-Term Ecological research sites*. Ed. D. Greenland. Institute of Arctic and Alpine Research. University of Colorado. Occasional Paper No 44. pp 11-17.
- McKee, A., G. M. Stonedahl, J. F. Franklin, F. Swanson. 1987. Research publications of the H.J. Andrews Experimental Forest, Cascade Range, Oregon, 1948 to 1986. General Technical Report. PNW-GWT-201. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 74 pp.
- Namias, J. 1959. Recent seasonal interactions between North Pacific waters and the overlying atmospheric circulation. *Journal of Geophysical Research*. 64(6):631-646.
- _____. 1968. The labile Gulf of Alaska cyclone—key to large scale weather modification elsewhere. *Proceedings of the International Conference on Cloud Physics*, August 26-30, 1968. Toronto, Canada 735-746.
- _____. 1969. Seasonal interactions between the North Pacific Oceans and the atmosphere during the 1960s. *Monthly Weather Review*. 97(3):173-192.
- _____. 1971. The 1968-69 winter as an outgrowth of sea and air coupling during antecedent seasons. *Journal of Physical Oceanography*. 1(2):65-81.
- _____. 1972. Experiments in objectively predicting some atmospheric and oceanic variables for the winter 1971-72. *Journal of Applied Meteorology*. 11(8):1164-1174.
- _____. 1978. Multiple causes of the North American abnormal winter 1976-77. *Monthly Weather Review*. 106(3):279-295.
- _____. 1979. Premonitory signs of the 1978 break in the West Coast Drought. *Monthly Weather Review*. 107(12):1676-1681.
- _____. 1981. The heavy California winter rains of 1979-80 as a manifestation of macroscale air/sea coupling. *Proceedings of the Fifth Annual Diagnostics Workshop*. Joint Institute for the Study of Atmosphere and Ocean, University of Washington, Oct 22-24. 1980. U.S. Dept. Comm. NOAA.
- Pacific Northwest Rivers Commission. 1969. *Climatological Handbook of the Columbia Basin States*. 3 vols. Private publication by the PNW Rivers Commission.
- Phillips, E. L. 1960. *Climates of the States* No. 60-45: Washington. pp 1042-1049 in *Climates of the States*. Vol 2. Gale Research Company. Detroit.
- Redmond, K. T. 1985. An inventory of climate data for the state of Oregon. Report SCP-3. Office of the State Climatologist. Climatic Research Institute. Oregon State University. Corvallis. Oregon. 160 pp.
- Redmond, K. T., and R. W. Koch. 1991. Climate and stream-flow variability in the western United States and their relationship to large-scale circulation indices. *Water Resources Research*. 27(9):2381-2399.
- Roden, G. I. 1989. Analysis and interpretation of long-term climate variability along the West coast of North America. In *Aspects of climate variability in the Pacific and western Americas*. Ed. D.H. Peterson. American Geophysical Union. 445 pp. pp 93-111.
- Ropelewski, C. F. and M. S. Halpert. 1986. North American precipitation and temperature patterns associated with the El Niño/Southern Oscillation (ENSO). *Monthly Weather Review*. 114:2352-2362.
- Sternes, G. L. 1960. *Climates of the States*. No. 60-35: Oregon. pp 806-811. in *Climates of the States*. Vol 2. Gale Research Company. Detroit.
- Wallace, J. M. and D. S. Gutzler 1981. Teleconnections in the geopotential height field during the Northern Hemisphere winter. *Monthly Weather Review*. 109:784-812.
- Walsh, J. E. and M. B. Richman. 1981. Seasonality in the Associations between Surface Temperatures over the United States and the North Pacific Ocean. *Monthly Weather Review*. 109:767-783.
- Waring, R. H., H. R. Holbo, R. P. Bueb, and R. L. Fredrikson. 1978. Documentation of meteorological data from the Coniferous Forest Biome primary station in Oregon. General Technical Report. PNW-73. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 23 pp.
- Wigley, T. M. L., P. D. Jones, K.R. Biffra, and G. Smith. 1990. Obtaining sub-grid scale information from coarse-resolution General Circulation Model output. *Journal of Geophysical Research*. 95(D2):1943-1953.
- Yarnal, B. and H. F. Diaz. 1986. Relationships between extremes of the Southern Oscillation and the winter climate of the Anglo-American Pacific Coast. *Journal of Climatology*. 6:197-219.

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Richy J. Harrod, U.S. Forest Service, Leavenworth Ranger District, Leavenworth, Washington 98826

and

Ronald J. Taylor, Department of Biology, Western Washington University, Bellingham, Washington 98226

Reproduction and Pollination Biology of *Centaurea* and *Acroptilon* Species, with Emphasis on *C. diffusa*

Abstract

Reproduction and pollination of *Centaurea diffusa*, *C. maculosa*, *Acroptilon repens*, and *C. solstitialis* were examined. Based on controlled pollination, *Centaurea diffusa*, *C. maculosa*, and *A. repens* were found to be obligate outcrossers; whereas *C. solstitialis* proved to be facultatively xenogamous. The importance of floral visitors was determined by visitation frequency along established transects and by pollen load analyses. Principal visitors to at least three of the four species were *Bombus* spp., *Anthophora* sp., *Apis mellifera*, and *Megachile* sp. None of the important flower visitors of *C. diffusa* discriminated between white and purple flower heads. Time of day did not significantly influence visitation, except for *Anthophora* sp. which visited primarily in the morning. Nectar analyses showed sucrose and fructose in a ratio of approximately 2:1 to be the major sugars in three of the species. In *A. repens*, glucose was also present (sucrose: fructose: glucose; 2:1:1). The open recombination systems of *Centaurea diffusa*, *C. maculosa*, and *A. repens* promotes genetic diversity allowing invasion of natural habitats. The annual habit and versatile breeding system of *C. solstitialis* contributes to its success as a noxious weed. *Apis mellifera* may increase the reproductive capacities of knapweeds.

Introduction

The knapweeds (three *Centaurea* species and *Acroptilon repens*) examined in this study are of great importance in western North America because of their status as noxious weeds. They have expanded rapidly on rangelands of the Northern Intermountain Region since their introduction from Eurasia during the early 1900's (Cranston 1980, Roché *et al.* 1986, Roché and Talbott 1986). The knapweeds are competitive and often trigger ecosystem degradation by displacing native vegetation, decreasing biodiversity, contributing to soil erosion (Maddox 1979, Cranston 1980, Tyser and Key 1988), reducing the economic value of ranges (Strang *et al.* 1979) and decreasing recreation and property values (Talbott Roché and Roché 1988).

As is true of other successful weeds, the knapweeds combine many morphological and physiological characteristics which allow them to quickly occupy and persist in disturbed habitats. Such characteristics include high seed production (Watson and Renney 1974, Schirman 1981, Roché *et al.* 1986, Callihan *et al.* 1989); successful seed dispersal (Watson and Renney 1974, Roché 1992); discontinuous seed germination and germination over a broad range of temperatures (Watson and Renney 1974, Watson 1980, Callihan *et al.* 1989, Taylor and Harrod, unpublished study); and allelopathy (Watson and Renney 1974, Muir and Majak 1983).

Other characteristics of knapweeds which may or may not relate to their success as weeds fall in the general category of reproductive and pollination biology. The knapweeds are discussed frequently in the literature, but their pollination biology has received little attention. Watson and Renney (1974) noted that the knapweeds are entomophilous and self-compatible, but they did not go into further detail about specific floral visitors nor did they provide supporting data. Proctor and Yeo (1979, and references cited therein) refer to visitation of several insects to *Centaurea* species but provide no quantitative data.

Our study was designed to answer the following questions: Are these four knapweed species self-compatible, and if so, can they be self-pollinated in the absence of insect visitors? What are the important insect visitors? What is the visitation constancy of the representative insects? Is insect visitation influenced by time of day (see McCall and Primack 1992)? What floral rewards are being collected by the various insect visitors? What are the types and ratio of sugars present in nectar rewards of the species and does there appear to be a relationship between these sugars and insect visitors along the lines suggested by Percival 1960, Baker and Baker 1975, Faegri and van der Pijl 1979?

Flower color varies in some *Centaurea* species, especially *C. diffusa* which has both white and

purple forms. Pollinator preference for a particular color morph could lead to greater reproductive success of that form (Kay 1978, Stanton 1987). Thus, in the context of the questions stated above, we wanted to know if flower visitors discriminate between white- and purple-flowered forms of *C. diffusa*.

Methods

Study Sites

The study sites were located in Okanogan National Forest, near Winthrop, Washington (diffuse knapweed *Centaurea diffusa* Lam.); in Lolo National Forest, near Missoula, Montana (spotted knapweed *C. maculosa* Lam.); on private land near La Grande, Oregon (yellow starthistle *C. solstitialis* L.); and on private land near Haines, Oregon (Russian knapweed *Acroptilon repens* (L.) DC.). For more precise locations, see Figure 1. At each study site, the species studied was the dominant plant. The populations were extensive, although the areas studied were approximately 2500 m².

Pollination Studies and Fertility Analyses

At each site, 1 x 1 x 1 m cages were used to exclude insects from selected plants. The cages consisted of wooden frames covered by 1 x 1 mm mesh window screens. At the Haines, La Grande, and Missoula sites, four cages were set up, each enclosing a single plant. Criteria used in selecting plants included: (1) plant size—large enough to have numerous heads but small enough to fit in the cage; (2) location—well within the population, avoiding “edge effect”; (3) pre-anthesis developmental stage—opened heads, if any, were removed; and (4) sufficient spatial separation from other caged plants to ensure independent samples. At the Washington (*C. diffusa*) site, eight white- and eight purple-flowered plants were randomly selected and caged prior to opening of flower heads. The field work was carried out from mid June through August, 1989, at the Oregon and Montana sites, and from mid June through September, 1990, at the Washington site.

At the Oregon (*A. repens* and *C. solstitialis*) and Montana (*C. maculosa*) sites, all controlled pollinations involved caged plants. In each of three cages, ten heads were selfed via geitonogamy (pollination of flowers on the same plant) and ten outcrossed (xenogamy), by picking flowering heads of

non-caged plants and gently rubbing these over the florets of selected heads of caged plants. To avoid pollen contamination, geitonogamy and xenogamy were carried out on different days. All pollinated heads were appropriately tagged. The fourth cage at each of the three sites, in addition to untreated heads on the other three caged plants, was used to test autogamy (pollination in the same flower), i.e. the plants or heads were left untouched.

At the Washington (*C. diffusa*) site, autogamy, geitonogamy and xenogamy were compared by randomly selecting eight white-flowered plants and eight purple-flowered plants for each reproductive treatment. To test for autogamy, exclusion cages were placed around the sixteen selected plants, as noted above, and left untouched. Exclusion cages were not used in other tests. To test for geitonogamy, small cotton bags were placed over two unopened but similarly developed flower heads of each of the sixteen selected plants. Bags were briefly removed to hand pollinate flowers when anthers were dehiscing and stigmas were presumed to be receptive, i.e. the heads were gently rubbed together. Bags were left on until after the heads had closed and the corollas had become senescent. Two non-bagged open pollinated heads were selected and tagged from each of the additional sixteen plants, providing the opportunity for xenogamy.

Heads from all treatments were collected when mature and the seeds were counted. From each of the *C. maculosa*, *A. repens*, and *C. solstitialis* populations, 120 heads were collected: 30 representing geitonogamy; 60 representing xenogamy (30 from caged plants and five randomly collected from each of six non-caged plants); and 30 representing autogamy (15 from the single, “autogamous” caged plant, and five non-manipulated heads from each of the other three caged plants, all randomly collected). Seed count data of each population were subjected to a 1 x 4 factorial analysis of variance (ANOVA), factor 1 being species and the four levels of factor 2 being autogamy, geitonogamy, open-pollination, and xenogamy (bagged heads). If the probability of a Type I error was 5% or less, the result was considered to be significant.

From the *C. diffusa* population, 96 seed heads were chosen at random, two from each of the 48 plants selected for autogamy, open pollination, and geitonogamy (16 plus 16 plus 16). The 32 open-pollinated heads were selected randomly prior to

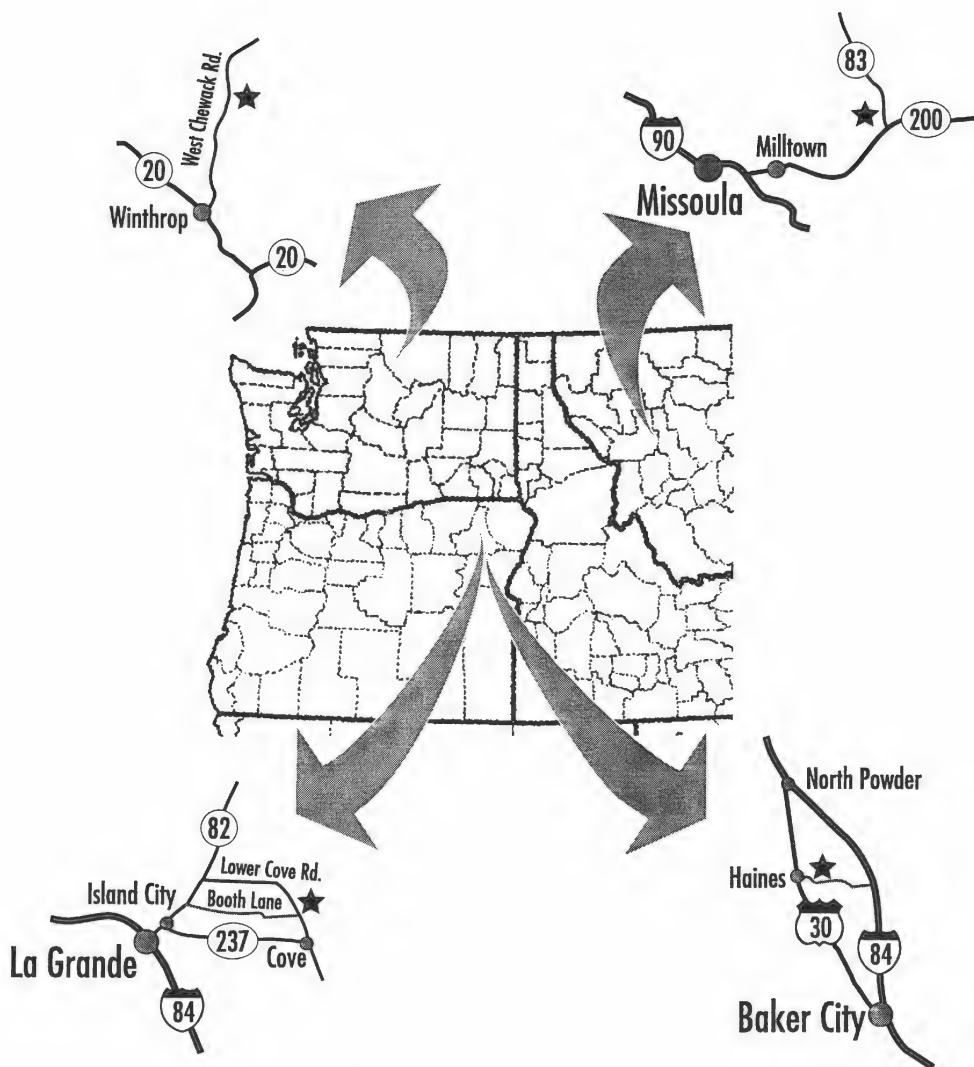


Figure 1. Location of study sites (★). The “diffusa” site is located on Forest Service land 8 miles north of Winthrop, Washington, on West Chewach Road. The “maculosa” site is located on state land northeast of Milltown, Montana, on Highway 83 approximately 2 miles north of Highway 200. The “repens” site is located on private land by following 3rd Street 5 miles east of Haines, Oregon. The “solstitialis” site is located on private land by following Booth Lane 4 miles east of Island City, Oregon, to Lower Cove Road.

pollination. Seed count data from this population were subjected to a 2 x 3 factorial ANOVA with subsampling ($\alpha = .05$). The two levels of factor 1 were flower head color, white, and purple. The three levels of factor 2 were reproductive treatments, autogamy, geitonogamy, and open pollination.

To test for the possibility of anemophily (wind pollination), a pollen sampler was operated for six hours (from 0900 to 1500) for each of three days during peak flowering (late July, early August) in the *C. diffusa* population. The pollen sampler was attached to a vacuum pump which was calibrated

at 486.5 L of air/hour. Pollen was deposited on a clear petroleum grease coated microscope slide which advanced every hour. At each hour, wind speed was recorded at canopy height using a turbine digital anemometer and was averaged for a five minute period.

Determination of Flower Visitor Frequency

Frequency of insect visits was measured along a 50m transect roughly through the center of each population. The transects were traversed once in the morning (ca. 0900) and once in the afternoon (ca. 1500) for three consecutive days in the *C. maculosa*, *A. repens*, and *C. solstitialis* populations, and for a total of ten times at various dates (late July, early August) during flowering in the *C. diffusa* population. One minute was spent at each meter along the transect, counting the number of visits to capitula (heads) by insect species. Visits were counted only if they occurred within an area approximately 200 x 20 cm, centered on and perpendicular to the transect line. A visit involved physical contact by the insect with any flower of the capitulum. For *C. diffusa*, numbers of visits per meter per minute, morning and afternoon, were analyzed using a 2 x 9 (*C. diffusa*, *C. maculosa*, *C. solstitialis*) and a 2 x 12 (*A. repens*) factorial ANOVA ($\alpha = .05$). Morning and afternoon were the two levels of factor 1 and the nine or twelve levels of factor 2 represented different insect species.

A representative sample of insects visiting the respective knapweed species was collected from each population. The insects were killed using ethyl acetate and allowed to dry. The pollen was later scraped from the head, abdomen, and legs, and placed on a microscope slide in a small amount of 30 percent glycerol in distilled water, with two crystals of thymol (following Puris *et al.* 1964). We counted up to 100 pollen grains at 100x or 400x from a few random locations on the slide; or when fewer than 100 grains were present, all were counted. Pollen grains were identified using permanent reference pollen mounts of knapweed and associated species. Differences among visitors based on pollen load purity for each species were analyzed using a complete randomized design, ANOVA ($\alpha = .05$).

In the *C. diffusa* population, we determined if insects discriminated between white- and purple-flowered plants. Ten equally spaced (ca. 1 m apart)

combinations of two white-flowered plants and one purple-flowered plant, and ten combinations of two purple-flowered plants and one white-flowered plant were selected for a total of 20 experimental sets. For each experimental set, one plant, white- or purple-flowered, served as a "subject" plant and two plants, one of each flower color type, served as "choice" plants. Color preference was recorded only when an insect would visit the subject plant and then select one of the choice plants. Insect observations were made for one hour both in the morning (ca. 0900) and afternoon (ca. 1500). Differences among insects based on color preference and time of day were analyzed using a 2 x 2 x 2 x 2 factorial ANOVA ($\alpha = .05$). The levels of factor 1 were color of the "subject" plant (white or purple), levels of factor 2 were colors of "choice" plants (white or purple), levels of factor 3 were morning and afternoon, and levels of factor 4 were insect species.

Nectar Analysis

The sugar constituents of nectar were determined by paper chromatography. Eight mature plants of each species and flower color (*C. diffusa*) were selected at random and four to six flowering head of each plant were used per nectar sample. To access the nectar, the upper part of the corolla tubes, along with the anthers and styles, were cut away with a sharp knife. The nectar was then squeezed out into a spot on Whatman #1 chromatography paper. Spotting was done both in the morning (ca. 0900) and afternoon (ca. 1500) of the same day for a total of 16 nectar samples from each population and floral color. Standards of approximately 2% glucose, fructose, and sucrose were later spotted alongside nectar samples. Ascending chromatography was used to separate sugars (Markham 1982). Nectar sugars were identified by comparing spot colors (following treatment with a reagent (Markham 1982)) and rate of flow to the standard sugars. Color intensities were used to determine the relative concentration of the nectar sugars.

Results

Wind-borne Pollen

A mean of 22 (sd, ± 15.9) pollen grains of *C. diffusa* was fixed on the slides of the pollen sampler per hour of operation. There was no apparent correlation between wind speed or time of day and pollen numbers.

TABLE 1. Mean numbers¹ of seeds per head for the four knapweed species, with *C. diffusa* separated into white and purple color forms, in response to different pollination treatment.

Species	Treatment			
	Autogamy	Geitonogamy	Outcrossed	Open pollinated
<i>C. diffusa</i>				
white	1.0	0.2	n/a	7.1
purple	1.2	0.2	n/a	10.6
<i>C. maculosa</i>	1.1	1.0	22.0	24.5
<i>C. solstitialis</i>	10.4	18.9	34.6	56.5
<i>A. repens</i>	1.8	1.1	10.3	20.1

¹For each species, underlined values are *not* significantly different from one another.

Seed Production

Based on seed production in response to the various pollination treatments, *C. diffusa*, *C. maculosa*, and *A. repens* are obligately xenogamous (Table 1). The few seeds that were produced autogamously and geitonogamously could have resulted from anemophily since the presence of wind-blown pollen was confirmed. The fewer seeds produced in bagged vs. caged capitula of *C. diffusa* also suggests this, although the differences were not significant. In *C. maculosa* and *A. repens*, open pollinated heads produced significantly more seeds than caged, crossed heads, probably because hand-pollinated plants were pollinated once, whereas open-pollinated plants could have received numerous visits.

Centaurea solstitialis produced significantly more seeds by xenogamy than by other treatments, but it must be concluded that the species is facultatively autogamous, and the greater number of seeds set by geitonogamy than by autogamy can probably be attributed to more pollen deposited on the stigmas and thus greater opportunity for self-compatibility (Table 1).

Open pollinated purple-flowered plants of *C. diffusa* set significantly more seed than white-flowered plants, even though white-flowered plants out-numbered purple-flowered plants by a ratio of 3.2:1 and major insect visitors did not discriminate according to color (see below).

Floral Visitation

The various insects collected from the flowers of the four knapweed species are listed in Table 2

with the purity of pollen loads provided. The purity of pollen carried by honey bees (*Apis mellifera*), a species of digger bee (*Anthophora* sp. 1), bumble bees (*Bombus bifarius nearcticus* and *B. occidentalis*), and a species of leafcutting bee (*Megachile* sp.) was significantly greater than other species. However, there was a considerable amount of overlap in the multiple range tests and several species of *Bombus*, *Anthophora* sp. 2, various bees of the families Megachilidae and Halictidae, and some of the syrphid flies also carried relatively pure loads of knapweed pollen. Other insects were infrequent visitors or carried very little knapweed pollen, as was the case of lepidopterids. Most of the important floral visitors exhibited a high degree of constancy as noted by pure pollen loads, although there were exceptions, such as *Megachile* sp. (Table 2).

Based on transect samples (Table 3), *Apis mellifera* dominated the visitor faunas of all knapweed species except *A. repens* which was most frequently visited by *Megachile*. The second, significantly most frequent visitors were *Bombus bifarius* (at the *C. maculosa* site), *B. huntii* (at the *A. repens* site), *B. occidentalis* (at the *C. solstitialis* site), and *Anthophora* sp. 1 at the *C. diffusa* site. Among the important visitors, only *Anthophora* sp. 1 and *Bombus huntii* differed significantly in the time of their visits, both favoring morning over afternoon.

Only *Apis mellifera* and *Anthophora* sp. 1 visited *C. diffusa* in sufficient numbers to assess their color discrimination. Based on number of visits per hour, neither showed a significant preference for flower color, nor did time of day influence color choice. Based on observations made in the

TABLE 1. Insects collected from heads of knapweed species and purity of pollen loads. Data represent mean numbers based on counts up to 100 grains from each of ten individuals, or fewer in cases when specimens were limited.

Insect taxa ORDER—family—sp.	Knapweed pollen ¹ /foreign pollen/# insects ¹			
	diffusa	macul.	repens	solst.
HYMENOPTERA—Apidae				
<i>Apis mellifera</i>	100 ^a /1/10	100 ^a /2/10	-----	100 ^a /1/10
<i>Bombus bifarius</i>	86 ^{ab} /2/08	84/1/06	100 ^a /3/05	93 ^a /1/06
<i>Bombus occidentalis</i>	89 ^{ab} /1/10	58/2/05	-----	62/1/05
<i>Bombus huntii</i>	-----	-----	87 ^b /5/08	-----
<i>Bombus centralis</i>	-----	-----	-----	88/2/04
<i>Bombus fervidus</i>	91/0/03	-----	-----	-----
<i>Bombus flavifrons</i>	48/52/01	-----	-----	-----
<i>Bombus vosnesenskii</i>	-----	-----	-----	100/0/01
—Anthophoridae				
<i>Anthophora</i> sp. 1	97 ^a /3/10	100 ^a /9/10 ²	100 ^a /3/05	88 ^a /24/05 ⁴
<i>Anthophora</i> sp. 2	66 ^{bc} /1/10	-----	100 ^a /2/02	-----
—Megachilidae				
<i>Megachile</i> sp.	88 ^{ab} /12/05	100 ^a /8/05	100 ^a /0/10	100 ^a /9/08 ⁴
<i>Osmia</i> sp.	88/12/02	-----	-----	-----
unknown sp.	50 ^c /2/05	-----	-----	-----
—Halictidae				
unknown sp. 1	-----	-----	82/5/06	51/15/04 ⁴
unknown sp. 2	-----	-----	-----	02/0/01
<i>Agopastemon</i> sp.	-----	-----	65/1/02	-----
—Colletidae				
unknown sp.	-----	-----	76/45/02 ⁵	-----
—Sphecidae				
<i>Bembix</i> sp.	78/22/01	-----	-----	-----
unknown sp.	-----	01/3/01	18/1/01	-----
<i>Sceliphron</i> sp.	-----	-----	25/5/01	-----
—Vespidae				
<i>Vespa</i> sp.	-----	03/0/01	-----	-----
DIPTERA—Syrphidae				
<i>Eristalis arbustorum</i>	-----	-----	47/15/04	63/1/03
<i>Eristalis tenax</i>	00/0/01	-----	-----	28/7/03
<i>Eristalis hirtus</i>	-----	-----	100/12/02	-----
<i>Scaeva pyrastris</i>	-----	100/7/01	-----	20/3/02
<i>Helophilus fociatus</i>	-----	-----	75/33/04 ⁵	-----
—Bombyliidae				
<i>Systoechus oreas</i>	00/0/01	00/0/03	06 ^c /0/05	25/0/02
<i>Villa</i> sp.	14/0/01	08/2/02	-----	-----
—Tachinidae				
unknown sp.	-----	13/42/02 ⁵	63/38/04 ⁶	-----
LEPIDOPTERA-Hesperidae				
<i>Ochlodes sylvanoides</i>	13/2/02	04/0/02	-----	-----
—Lycanidae				
<i>Lycaena</i> sp.	-----	-----	04 ^c /3/06	-----
<i>Plebejus melissa</i>	14 ^d /2/09	-----	-----	-----
—Pieridae				
<i>Colias philodice</i>	25 ^d /1/10	-----	-----	-----
<i>Pontia protodice</i>	-----	-----	03/1/05	-----
—Satyridae				
unknown sp.	-----	04/7/01	-----	-----

¹a,b,c,d—For each knapweed species, means are *not* significantly different from each other. In *C. diffusa*, overlap in the Newman-Keuls multiple range test is indicated by double lettering. Fewer than five individual insects were not included in the statistical analyses.

²One specimen had a large load of *Hieracium* sp. pollen.

³Two specimens had large loads of *Cirsium vulgare* pollen.

⁴Some specimens had large loads of *Convolvulus arvensis* pollen.

⁵Some specimens had large loads of *Chrysothamnus viscidiflorus* pollen.

⁶Both specimens had large loads of *Lactuca serriola* pollen.

TABLE 3. Mean¹ morning (0900) and afternoon (1500) visits made to transect observation areas of the four *Centaurea* populations by various insects. The number of visits represents importance values of the potential pollinators.

Insect taxa	Transect visitations per population			
	<i>diffusa</i>	<i>macul.</i>	<i>repens</i>	<i>solst.</i>
<i>Apis mellifera</i>	38.4	42.4	0.0	25.3
<i>Bombus bifarius</i>	4.9	19.7	6.2	11.8
<i>Megachile</i> sp.	1.3	2.1	27.5	10.2
<i>Anthophora</i> sp. 1	8.4	11.3	5.8	4.7
<i>Bombus occidentalis</i>	0.3	7.4	0.0	19.8
<i>Bombus huntii</i>	0.0	0.0	13.1	0.0
Syrphidae ²	0.4	0.7	5.7	3.9
<i>Lycaena</i> sp.	0.0	0.0	8.3	0.0
<i>Halictid</i> sp.	0.0	0.0	4.9	3.0
Tachinidae	0.0	0.1	6.6	0.0
<i>Bombus centralis</i>	0.0	0.0	0.0	5.9
<i>Pontia protodice</i>	0.0	0.0	5.0	0.0
<i>Systoechus oreas</i>	0.0	0.4	0.8	0.3
<i>Anthophora</i> sp. 2	0.3	0.0	0.4	0.0
<i>Villa</i> sp.	0.5	0.0	0.2	0.0
<i>Bombus fervidus</i>	0.3	0.0	0.0	0.0
<i>Ochlodes sylvanoides</i>	0.0	0.3	0.0	0.0

¹Mean values represent multiple a.m. and p.m. transects in respective populations. In only three cases did a.m. and p.m. values differ significantly: (1) *Anthophora* sp. 1 visited more frequently in the a.m. at the *diffusa* and *maculosa* sites; (2) *Bombus huntii* was observed more frequently in the a.m. at the *repens* site; (3) the tachnid fly was observed more frequently in the p.m. at the *repens* site.

²*Eristalis* spp., *Scaeva pyrastris* and *Helophilus fociatus* are included in this family group.

field, the same can be said for other insects visiting *C. diffusa*. The general trend for pollinators was to visit several heads of the same plant and then fly to the next closest plant, regardless of its flower color. The only exceptions were the Lepidopterids which visited sporadically.

Nectar Analysis

Chromatographic analyses showed the nectar to consist of sucrose and fructose in a 2:1 ratio in *C. diffusa*, *C. maculosa*, and *C. solstitialis*. In *A. repens*, glucose was detected in small quantities (sucrose:fructose:glucose; 2:1:1). The similarity of sugar type and concentration between morning and afternoon samples (and between flower color in *C. diffusa*) helps to explain the general lack of visitation discrimination by major visitors.

Discussion

Autogamy may function to promote population establishment and most weeds are obligately or facultatively autogamous (see Allard 1965, Baker 1965, Stebbins 1965, Mulligan and Findlay 1970). How-

ever, inbreeding restricts recombination and, accordingly, limits adaptability. For most weeds this seems not to be a serious compromise because they have broad ecological tolerances (Baker 1965, Taylor 1990) and can exploit a variety of open habitats. The knapweeds examined in this study are somewhat exceptional in that they are obligate or preferential (*C. solstitialis*) outcrossers. This open recombination system may limit reproductive success of isolates but promotes genetic diversity allowing invasion of natural habitats.

Although self-compatibility had been reported in *Centaurea* species (Watson and Renney 1974), many species are nearly completely self-incompatible (Marsden-Jones and Turrill 1954, Lack 1976, 1982). Roché (personal communication) noted that *C. diffusa*, *C. maculosa*, and *A. repens* appear to be self-sterile and *C. solstitialis* nearly so. The potential for selfing in *C. solstitialis* suggested by our study, may be correlated with its annual habit. According to Grant (1981), autogamy is a particularly common and adaptive trait of annuals. In any case, the versatile breeding system

of *C. solstitialis* must contribute to its success as a noxious weed in the Pacific Northwest.

Most weeds have a generalist pollination strategy, that is, they can be successfully pollinated by a variety of insect types, an adaptive trait of colonizing species (Allard 1965, Baker 1965). In knapweed species, the pollen is openly presented and readily accessible to all pollen-foraging Coleoptera, Diptera, and Hymenoptera. On the other hand, nectar is concealed in short, narrow corolla tubes which also attracts "specialist" pollinators known for their high degree of floral constancy. In their comprehensive treatment of *Centaurea*, Marsden-Jones and Turrill (1954) list numerous floral visitors from several Orders, including "generalists" and "specialists," many of the same genera collected by us. Finally, the fact that knapweed species flower later in the summer than most associated species probably reduces competition for pollinators and increases constancy and reproductive success.

The importance of the respective insect visitors concentrating on the *Centaurea* and *Acroptilon* populations of our study can be judged by a combination of: (1) visitation frequency—as measured in transect observation areas; and (2) constancy—as determined by purity of knapweed pollen. It should be noted that our data do not provide direct evidence for the relative success of floral visitors as pollinators. It is known that frequent visitors are sometimes poor pollinators (Faegri and van der Pijl 1979). However, the open flower structure of the knapweeds likely promotes effective pollination by any visitor.

In three of the four populations (*A. repens* excluded), *Apis mellifera* was the most frequent visitor by all criteria. This species was present throughout the flowering season (at least at the *C. diffusa* site) and exhibited slow, deliberate manipulation and probing of florets. This behavior likely makes the species an important pollinator. It foraged throughout the day, primarily for nectar but some individuals collected pollen. *Apis mellifera* is an important pollinator of other *Centaurea* species including *C. jacea* and *C. nemoralis* (Marsden-Jones and Turrill 1954), *C. nigra* (Lack 1976), and *C. solstitialis* (Gary *et al.* 1980).

Considering all *Centaurea* and *Acroptilon* populations, bumblebees (*Bombus* spp.) were the second most important frequent visitors. These bees foraged on nectar, apparently exclusively, and exhibited a high degree of constancy suggesting that they are also important pollinators. The nectar of the *Centaurea* and *Acroptilon* species was found to be sucrose dominant, typical of flowers visited by bumblebees (Baker and Baker 1975, Faegri and van der Pijl 1979).

Other frequent visitors, listed in apparent order of importance, were solitary bees (*Anthophora*, *Megachile*, and colletids), halictids and syrphid flies, all pollen foragers. Butterflies were frequent visitors, feeding on nectar, but they carried little pollen and were probably of minor importance as pollinators.

Finally, there was the question of color preference among pollinators in *C. diffusa*. Observation and statistical analysis indicated that at least the major visitors did not discriminate by color. In the absence of favoritism for the white flower color and the significantly greater seed production of the purple form, it would seem that the population structure would shift toward the purple flower color. Perhaps it does but the greater numbers of white capitula in this population (3.2 white/1 purple) and in others observed but not analyzed suggests not. This apparent anomaly could relate to allele frequency of colonizers; greater fitness of white flowered plants (white color alleles linked with genes promoting fitness); greater predation of white flowers by fly larvae (a statistical analysis suggests not); or inadvertent sampling error. Further work is needed to distinguish among these possibilities.

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Literature Cited

- Allard, R. W. 1965. Genetic systems associated with colonizing ability in predominantly self-pollinated species. In H. G. Baker and G. L. Stebbins (eds.) The genetics of colonizing species, Academic Press, New York. Pp. 50-76.
- Baker, H. G. 1965. Characteristics and modes of origin of weeds. In H. G. Baker and G. L. Stebbins (eds.) The genetics of colonizing species, Academic Press, New York. Pp. 147-172.
- Baker, H. G. and I. Baker. 1975. Studies of nectar-constitution and pollinator-plant coevolution. In L. E. Gilbert and P. H. Raven (eds.) Coevolution of animals and plants, University of Texas Press, Austin. Pp. 100-140.
- Callihan, R. H., F. E. Northam, J. B. Johnson, E. L. Michalson, and T. S. Prather. 1989. Yellow starthistle—biology and management in pasture and rangeland. University of Idaho, Cooperative Extension Service, CIS No. 634.
- Cranston, R. 1980. Knapweed, its cause and effect in British Columbia. Knapweed Action Committee, Ministry of Agriculture, British Columbia.
- Faegri, K. and L. van der Pijl. 1979. Pollination ecology (3rd ed). Pergamon Press, Oxford.
- Gary, N. E., P. C. Witherell, and K. Lorenzen. 1980. Distribution of foraging honey bees to multiple, small floral plots of various species. *Envir. Entom.* 9: 43-46.
- Grant, V. 1981. Plant speciation. Columbia University Press, New York.
- Kay, Q. O. N. 1978. The role of preferential and assortative pollination in the maintenance of flower colour polymorphisms. In A. J. Richards (ed.) Pollination of flowers by insects, Academic Press, New York. Pp. 175-190.
- Lack, A. J. 1976. Competition for pollinators and evolution in *Centaurea*. *New Phytol.* 77: 787-792.
- . 1982. Competition for pollinators in the ecology of *Centaurea scabiosa* L. and *Centaurea nigra* L. III. Insect visits and the number of successful pollinations. *New Phytol.* 91: 321-339.
- Maddox, D. M. 1979. The knapweeds—their economics and biological control in the western states, U.S.A. *Rangelands* 1(4): 139-141.
- Markham, K. R. 1982. Techniques of flavonoid identification. Academic Press, New York.
- Marsden-Jones, E. M. and W. B. Turrill. 1954. British knapweeds; a study in synthetic taxonomy. Ray Society, London.
- McCall, C. and R. B. Primack. 1992. Influence of flower characteristics, weather, time of day, and season on insect visitation rates in three plant communities. *Amer. J. Bot.* 79(4): 434-442.
- Muir, A. D. and W. Majak. 1983. Allelopathic potential of diffuse knapweed (*Centaurea diffusa*) extracts. *Can. J. Plant Sci.* 63: 989-996.
- Mulligan, G. A. and J. N. Findlay. 1970. Reproductive systems and colonization in Canadian weeds. *Can. J. Bot.* 48: 859-860.
- Percival, M. 1950. Pollen presentation and pollen collection. *New Phyto.* 49(1): 40-63.
- Powell, R. D. 1990. The role of spatial pattern in the population biology of *Centaurea diffusa*. *J. Ecology* 78: 374-378.
- Proctor, M. and P. Yeo. 1979. The pollination of flowers. Collins Publ., London.
- Puris, M. J., D. C. Collier and D. Walls. 1964. Laboratory techniques in botany. Butterworths, London.
- Roché, B. F., Jr. 1992. Achene dispersal in yellow starthistle (*Centaurea solstitialis* L.). *Northw. Sci.* 66(2): 62-65.
- Roché, B. F., Jr. and C. J. Talbott. 1986. The collection history of *Centaureas* found in Washington state. Agric. Research Center, Res. Bull. XB0978. Wash. State Univ., Pullman.
- Roché, B. F., Jr., G. L. Piper, and C. J. Talbott. 1986. Knapweeds of Washington. *Coop. Ext. Bull.* 1393, Washington State University, Pullman.
- Schirman, R. 1981. Seed production and spring seedling establishment of diffuse and spotted knapweed. *J. Range Manag.* 34: 45-47.
- Stanton, M. L. 1987. Reproductive biology of petal color variants in wild populations of *Raphanus sativus*: I. Pollinator response to color morphs. *Amer. J. Bot.* 74(2): 178-198.
- Stebbins, G. L. 1965. Colonizing species of the native California flora. In H. G. Baker and G. L. Stebbins (eds.) The genetics of colonizing species, Academic Press, New York. Pp. 173-192.
- . 1970. Adaptive radiation of reproductive characteristics in angiosperms. I: Pollination mechanism. *Ann. Rev. Ecol. Syst.* 1: 307-326.
- Strang, R. M., K. M. Lindsay, and R. S. Price. 1979. Knapweeds: British Columbia's undesirable aliens. *Rangelands* 1: 141-143.
- Talbott, C. J. 1987. Distribution and ecologic amplitude of selected *Centaurea* species in eastern Washington. Wash. State Univ. Pullman. M.S. Thesis.
- Talbott Roché, C. J. and B. F. Roché, Jr. 1988. Distribution and amount of four knapweed (*Centaurea* L.) species in Eastern Washington. *Northw. Sci.* 62(5): 242-253.
- Taylor, R. J. 1990. Northwest weeds. Mountain Press Publ. Co., Missoula, Mt.
- Tyser, R. W. and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northw. Sci.* 62(4): 151-160.
- Watson, A. K. 1980. The biology of Canadian weeds. 43. *Acroptilon* (*Centaurea*) *repens*. *Can. J. Plant Sci.* 60: 993-1004.
- Watson, A. K. and A. J. Renney. 1974. The biology of Canadian weeds. 6. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* 54: 687-701.

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A Late Pleistocene Brown Bear (*Ursus arctos*) from Northwest Washington

Abstract

The discovery of a partial skull and eleven teeth of *Ursus arctos* in glacial sediments from Whidbey Island provides the earliest known record of brown bears in the Pacific Northwest. Although the early dispersal of *U. arctos* in North America remains enigmatic, the age and location of this specimen are consistent with the hypothesis that these bears emigrated to the middle latitudes of western North America from the Alaska/Yukon region at the close of the Ice Age.

Introduction

The discovery of a bear skull from Late Pleistocene strata in a coastal bluff 2 km south of Point Partridge, Whidbey Island, Washington (Figure 1) provides a significant new contribution to our knowledge of Ice Age life in the Puget Sound region, an area that contains extensive exposures of glacial and glaciomarine sediments, but few vertebrate fossils. Interpretations of prehistoric animal life in this region largely depend on inferences made from other regions where unusual environmental conditions produced great accumulations of bones, such as the tar seeps of southern California, guano deposits of the southwestern U.S., and the peat bogs and other sediments of Alaska and Yukon Territory. In contrast, skeletal remains from the Pacific Northwest are usually limited to disarticulated fragments that were dispersed prior to burial by streams or scavenging animals.

Ice Age vertebrate fossils have previously been reported from the Pacific Northwest by Scott (1967), Harington (1975), Newcomb and Repenning (1970), Peterson et al. (1983), and Rensberger et al. (1984), but this published record is far from complete. For example, a ground sloth skeleton (*Megalonyx* sp.) discovered in 1961 during construction of the Seattle-Tacoma Airport is a featured exhibit at the University of Washington Burke Museum, and the Western Washington University geology display collection includes a large mammoth tusk from the Skagit River valley found in 1979, and several mammoth bones excavated from central Washington in 1954; none of these specimens have been described in the scientific literature.

The Whidbey Island bear fossil was found in 1991 by D. J. Easterbrook and C. A. Carlstad,

who noticed two jaw fragments containing 4 large teeth exposed by coastal erosion along the contact zone between glaciomarine gravel and overlying dune sand. A more extensive search in 1993 yielded a large section of skull and 7 additional teeth (Figure 2, 3).

Description

The fossils consist of a large fragment of cranium, with the following teeth: C¹, P⁴, M¹, M², and alveoli for vestigial premolars P¹ and P³. Three detached upper incisors were found in the adjacent sediment. The dentition (Table 1) compares very closely in size and form to modern *Ursus arctos horribilis* (grizzly bear) specimens in the WWU mammal collection, the teeth being markedly larger than those of *U. americanus*, the modern black bear. They are discernably different from the two other bear species that inhabited the western U.S. during the Late Pleistocene, *Arctodus simus* Cope (short-faced bear) and *Ursus optimus* Schultz. The latter species was originally believed to be an ancestral black bear, later described as a variant of *U. americanus* (Kurtén and Anderson 1980). However, Graham (1991) considers *U. optimus* to represent a small-statured race of *U. arctos*. Based on enamel wear, the Whidbey Island bear was probably at full maturity, and perhaps of advanced age. The incisors have been abraded to about half of their original crown height, and upper left molar #1 contains a very large decay cavity that appears to have developed following fracture of a cusp. The upper left canine is broken at the tip, but the absence of wear marks on the adjacent enamel suggests this damage occurred following the death of the animal.

Geologic setting

The geology of Pleistocene and Holocene deposits of central Whidbey Island has been discussed in

¹Present address: 14815 104th Ave NE, Bothell, WA 98011

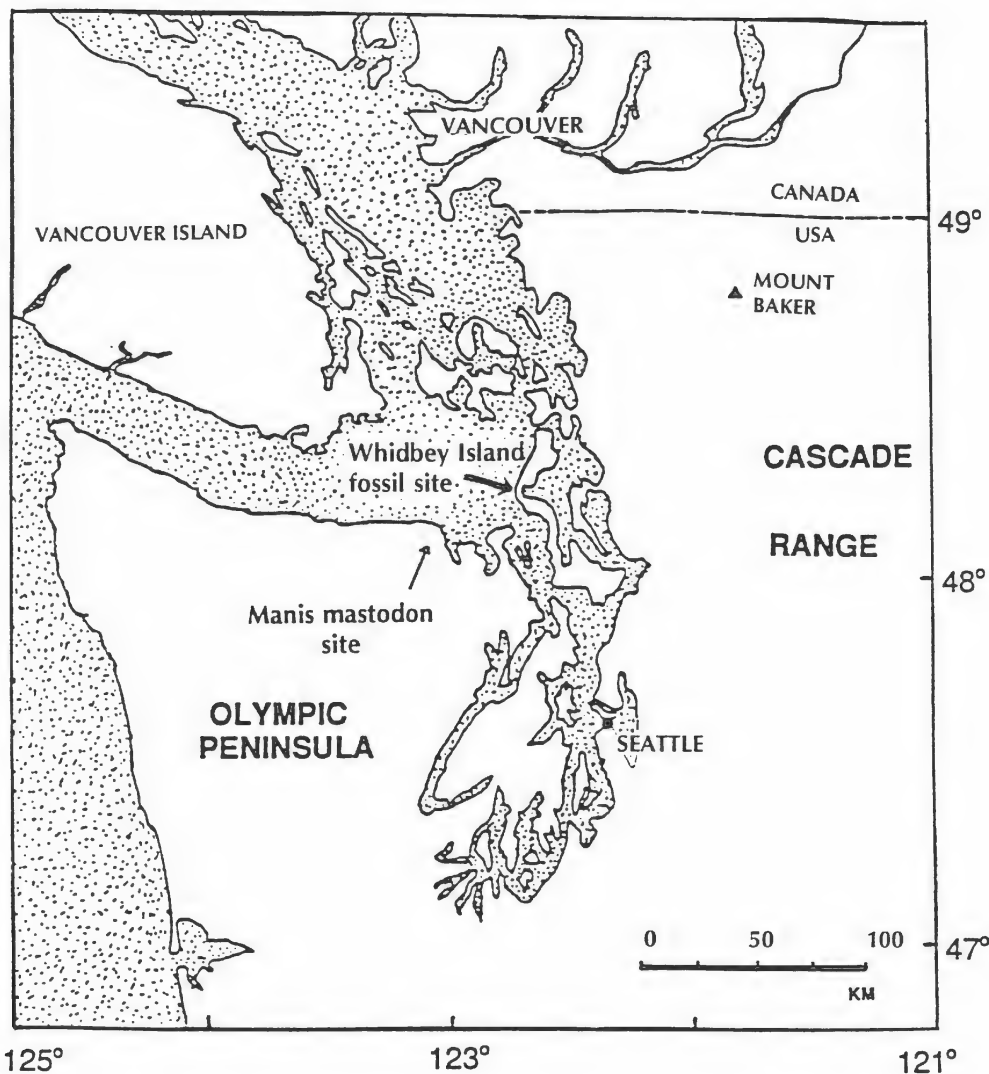


Figure 1. Location map.

detail by Easterbrook (1992) and Carlstad (1992). The fossil site occurs in an area of kettle topography that formed when the retreating ice and accompanying isostatic rebound combined to expose a 20-30 km wide zone of unforested lowland separating the waters of Puget Sound from the adjacent foothills of the North Cascade Range. The fossil appears to represent disarticulated skeletal material that accumulated in a kettle that was be-

ginning to be filled by dune sand. The thickness of the sand unit varies from 20 to 70 m, providing a prominent stratigraphic indicator of the abrupt transition from glaciomarine deposition to aeolian sedimentation following the final retreat of the ice sheet (Figure 4). Although no other large fossils have been found at this site, the sand beds contain widely scattered faunal remains, generally consisting of a single bird or rodent bone aligned

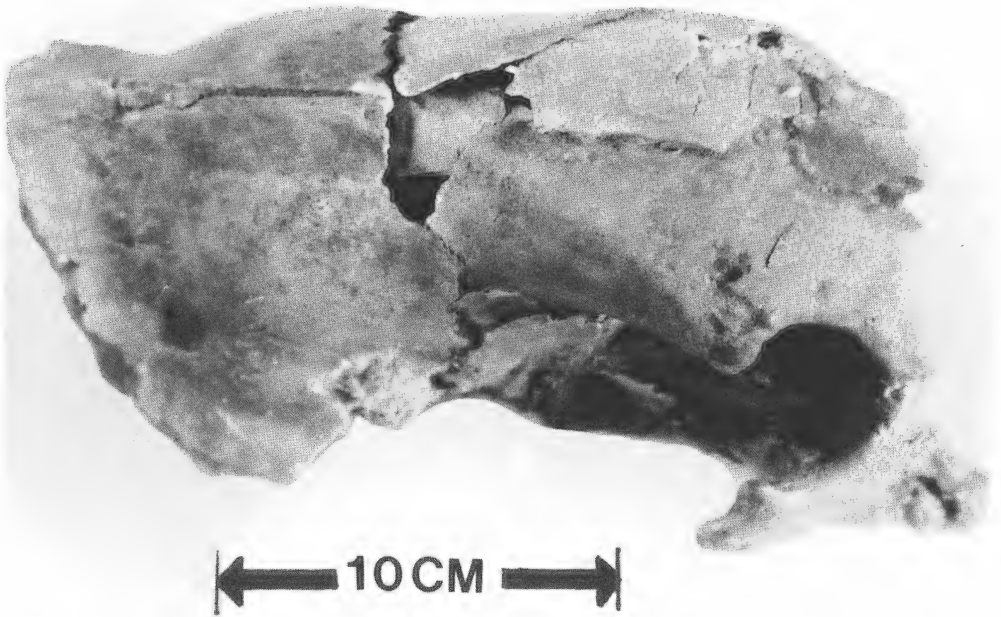


Figure 2. Dorsal view of parietal and frontal portion of bear skull from Whidbey Island. The anterior region has been destroyed by weathering; bones of the zygomatic arch appear to have been lost during sedimentary transport prior to final burial.

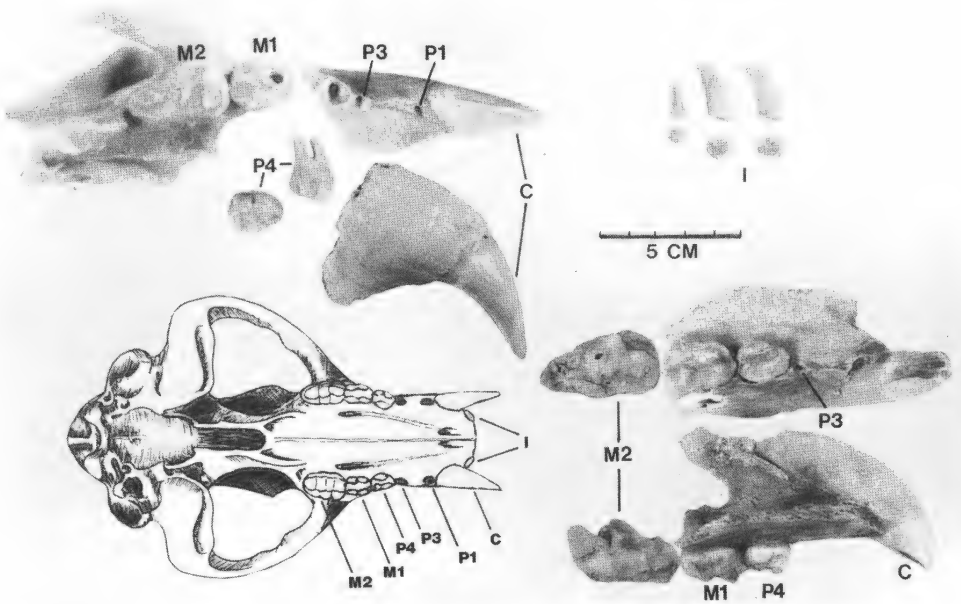


Figure 3. Ventral view of upper jaw, showing crown and profile views. I = incisors, C = canines, P1 and P3 = vestigial premolars, P4 = premolar, M1 and M2 = molars. Sketch of skull is reduced 0.5 X relative to photographs.

TABLE 1. Measurement of upper dentition of Pleistocene and Recent bears of western North America. Data were obtained by calculating the average of measurements for the right and left teeth, to compensate for very slight variations in shape and size.

Dimensions—mm	Whidbey Bear	<i>Ursus arctos horribilis</i> Ord Recent—Alaska				<i>Ursus americanus</i> Pallas Recent—Washington					<i>Arctodus simus</i> Cope Pleistocene—California				<i>Ursus optimus</i> Schultz (= <i>U. arctos</i> ?—see text) Pleistocene—California					
		WWU B-2295	WWU B-2121	WWU G-SKD	Mean	WWU B-1650	WWU B-143	WWU B-259	WWU B-2247	Mean	UC 33111	UC 3001	UC 3005	Mean	UC 2090	UC 16357	UC 24803	UC 4678	UC 20746	Mean
Skull length from anterior side of orbit to posterior end of occipital condyle	205 ¹	220	220	230	223	155	170	145	180	163	211 ²	—	—	—	220 ²	—	—	—	—	—
Canine—diameter at base of enamel	23.5	21	24	25	23.3	15	18	12	—	15	28.5	27.9	—	28.2	24.8	19.8	21.2	20.6	22.7	21.8
Premolar 4—greatest anteroposterior diameter	15	16	16.5	16	16.2	10	11	10	11	10.5	21	20.5	20.4	20.6	—	—	—	—	—	—
Premolar 4—greatest transverse diameter	14	12	13	12	12.3	8	9	8	8	8.3	15	15	15.3	15.1	—	—	—	—	—	—
Molar 1—greatest anteroposterior diameter	22	21.5	22	23	22.2	16.5	18	18	16	17.1	23.5	24	23.8	23.8	20.2	17	16.8	17	18	17.8
Molar 1—greatest transverse diameter	19	16	18	16.5	16.8	11.5	12.5	12	12.5	12.1	22.5	23	22.1	22.5	15	13	12.3	13	13	13.2
Molar 2—greatest anteroposterior diameter	38	36	35	32.5	34.5	23	24	24	24	23.8	33.9	35	33	34	33.1	26.7	26.5	26	28.2	28.1
Molar 2—greatest transverse diameter	19	18	18	18	18	14	16	13.5	12.5	14	22.2	22	21.4	21.9	17	15	15	14	15.8	15.4

¹Length of Whidbey skull has been somewhat reduced from post-burial compaction.

²Data for *A. simus* and *U. optimus* taken from Schultz (1938); skull lengths for UC 33111 and UC 2090 calculated from photographs.

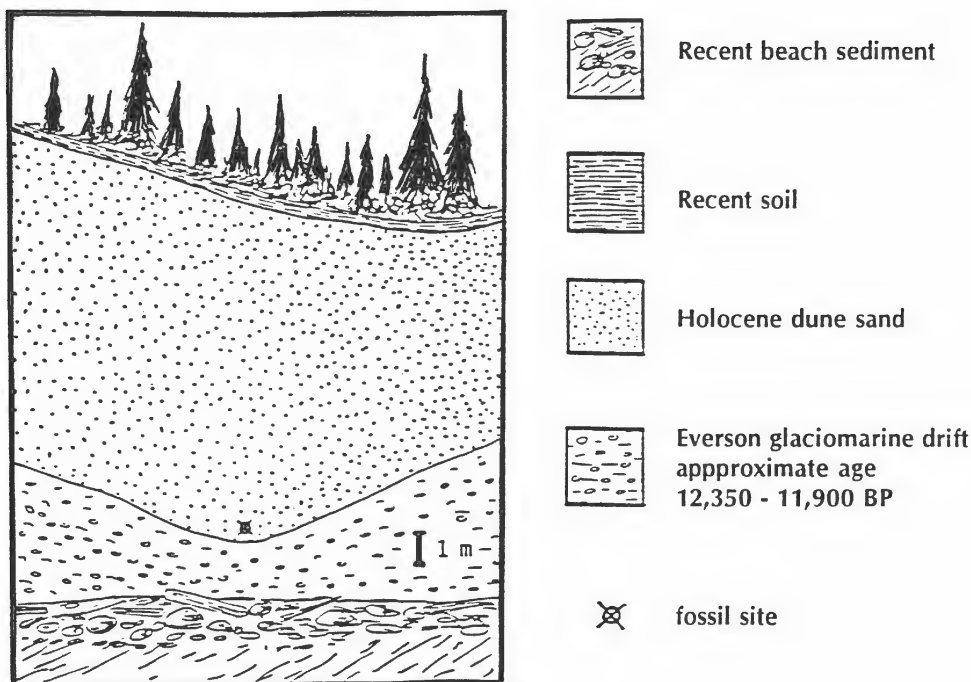


Figure 4. Stratigraphy of fossil site.

parallel to the sedimentary layering. Shells of terrestrial gastropods occasionally occur in the same strata.

The age of the Whidbey Island specimen is estimated at 12,000-11,500 BP, based on stratigraphic evidence. Glaciomarine drift underlying the fossil site contains mollusk shells that yield ^{14}C dates ranging from $12,350 \pm 400$ to $11,900 \pm 1700$ BP (Easterbrook 1992), and terrestrial habitat would not have existed during this phase of deposition. However, the sediment enclosing the fossil developed during the early phases of coastal uplift, at the onset of the extensive aeolian and fluvial deposition that had begun to dominate the region by about 11,000 BP. The age of the upper portion of the dune sand probably extends well into the Holocene, but no dates have been obtained from these strata.

Evolutionary history

The taxonomy of brown bears has undergone considerable revision since Merriam (1918) described 86 species and subspecies from North America

alone. These are all presently considered to constitute a single species, *Ursus arctos*, which also includes various European and Asian brown bears (Erdbrink 1953, Rausch 1963). Two subspecies are found in North America, *U. arctos horribilis* (grizzly) and *U. arctos middendorfi* (kodiak bear). Kodiak bears occur only on the coastal islands of Alaska, probably having evolved in the Late Pleistocene after glaciers isolated a local grizzly population. *Ursus arctos* subspecies can not reliably be distinguished by skeletal or dental characteristics, but the radiation of *U. a. horribilis* across much of North America at the close of the Pleistocene suggests that the Whidbey Island specimen represents a grizzly; *U. a. horribilis* has previously been described from Late Pleistocene asphalt deposits at McKittrick, California (Schultz 1938), and skeletal remains of grizzlies have been found at five archaeological sites in eastern Washington that range in age from 9,000 to 850 BP (Lyman 1968).

The discovery of the Whidbey Island fossil offers valuable insights into the dispersal of

U. arctos. The oldest known representative of the species is from China, dated at approximately 500,000 BP. These early brown bears appear to have descended from *U. etruscus*, a common early Pleistocene species recorded from Europe and Asia. *U. arctos* probably evolved from an Asian race of *U. etruscus* that became isolated when glaciers advanced southward from Scandinavia, and along the Ural Mountains. The date of origin of the new species is not known, but *U. etruscus* became extinct somewhere between 1.5 and 0.5 ma (Kurtén 1968, 1976).

U. arctos dispersed rapidly throughout Asia and Europe, eventually emigrating to North America when lowered sea level created a land bridge connecting Siberia and Alaska. Kurtén (1963, 1976) has suggested this migration occurred during the Wisconsin glaciation; two *U. arctos* specimens from the western Yukon show radiocarbon ages of $41,000 \pm 1,050$ and $36,000 \pm 1,150$ BP. After their arrival, brown bears inhabited the tundra region of southern Alaska and the Yukon, an area known as Beringia. This refugium provided a favorable but geographically isolated environment for moose, brown bear, and other animals that reached North America at a time when further southward dispersal was blocked by the Cordilleran Ice Sheet. In addition to the newly-arrived Asian emigrants, Beringia supported large populations of horses, bison, elephants, and many other species that occupied both the tundra of the far north and the grasslands that lay south of the zone of continental glaciation (Harington 1989, Pielou 1991).

The migration of *U. arctos* from Beringia to mid-continent locations is not fully understood. One interpretation (Kurtén 1976) is that the development of an ice-free corridor along the western margin of the Rocky Mountains at 12,000–11,000 BP allowed brown bears to reach an area near the present Montana-Alberta border. Humans may have followed the ice-free pathway during the same period, as suggested by Clovis-age sites scattered across the United States, including two locations in Washington (Gustafson et al. 1979, Mehringer 1988, Mehringer and Foit 1990). This hypothesis is clouded by the discovery of a fragment of humerus from a large bear in Middle Wisconsin till at Woodbridge, Ontario. Churcher and Morgan (1976) identified the specimen as *U. arctos*, and estimate the age at 50,000–40,000 BP. If these interpretations are correct, migration of the

species must have occurred earlier than previously believed, perhaps via an ice-free zone between the Laurentide ice sheet and the eastern flank of the Rocky Mountains (Hopkins 1967). Upon reaching the southern termini of the continental glaciers, brown bears were relatively unrestricted in their ability to travel. Late Pleistocene *U. arctos* fossils occur in Ontario (Peterson, 1965), Ohio (Miller 1899), Kentucky (Guilday 1968), Wyoming (Kurtén and Anderson 1974), and California (Kurtén 1960).

Although alpine glaciers occupied high valleys within the North Cascades, much of the mountain area remained ice-free during the Late Pleistocene, posing no formidable obstacles for bears on the move. The arrival of *U. arctos* in the Puget Sound lowlands is not surprising, since the region's temperate climate would have offered favorable habitat.

This westward migration is consistent with the behavior of modern grizzlies, which may travel considerable distances from season to season (Mundy and Flook 1973). Although the diet of these omnivores includes elk and other large mammals, as well as rodents, birds, and fish, much of their nutrition is obtained from plant material, particularly roots and berries. Mature coniferous forests provide scant food, and grizzlies are attracted to open areas where ample sunlight allows the development of understory vegetation. These conditions occur in subalpine meadows, along the margins of large lakes, and near the coast line, and it is in these environments where modern grizzlies are most abundant. Pleistocene brown bears displayed similar geographic preferences; fossils from 34 Danish sites indicate that from 11,500 to 4,500 BP, *U. arctos* migrated from inland locations to coastal habitats as forest density increased due to plant succession (Noe-Nygaard 1983).

Paleoenvironment

Environmental conditions at Whidbey Island were probably similar to the Manis Mastodon site on the Olympic Peninsula, 30 km to the southwest. Pollen and plant macrofossils show that the Manis area remained relatively treeless during the period from 12,000 to 11,000 BP, while other western Washington sites contained abundant conifers (Huesser 1977, Peterson et al. 1983). This difference was caused by the rain shadow of the Olympic Peninsula, as well as additional aridity caused

by the more southerly path of winter storm tracks in response to the proximity of the retreating ice sheet.

The 47 cm thick fossiliferous horizon at the Manis Mastodon site yields radiocarbon dates that range from $12,300 \pm 310$ to $11,000 \pm 150$ BP, presumed to be contemporaneous with the Whidbey Island bear fossil. In both locations, the Late Pleistocene topography consisted of gravel-floored ponds developed on stagnant ice terrain. Pollen at the Manis site indicates the shallow ponds were rich in aquatic plants, while adjacent uplands contained abundant shrubs and herbaceous plants. The plant assemblage appears to represent an early stage of succession as shrub willows (*Salix*), manzanita (*Arctostaphylos*) and other sun-loving species colonized the barren fields of till left by the retreating ice.

These environmental conditions would have provided an ecological magnet for newly-arrived brown bears, but the manner in which they reached Whidbey Island remains enigmatic. At present, the island is separated from the mainland by a 3 km wide channel to the east and the Olympic Peninsula lies 5 km to the southwest, distances that are within the swimming ability of modern bears (Heaton and Grady 1993). The age of the specimen does not allow sufficient time for significant plate tectonic activity to have occurred, but fluctuating sea levels may have temporarily reduced channel widths during the Late Pleistocene. Multiple strand lines on the mainland east of Whidbey Island are 35–67 m above present sea level, and date from about 12,000 to 11,500 BP (Easterbrook 1992). If this pattern of rapid emergence occurred at an erratic rate compared to eustatic sea level rise, portions of the shallow coast area fringing Whidbey

Island may have been temporarily exposed. Alternately, the 0.5 km channel at Deception Pass provides easy access to the mainland by way of Fidalgo Island. A final possibility is that *U. arctos* crossed from the mainland via ice blocks calved from the retreating ice sheet, which was located approximately 100 km to the north, near the present U.S.-Canada border.

Grizzlies survived the rigors of the last glaciation, and flourished in the mild climate of the Holocene, with an estimated population of 50,000 in the lower 48 states when Lewis and Clark visited in 1805. Due to combined impacts of unrestricted hunting and extensive habitat loss, by the 1930s *U. arctos* was extinct in the northwestern U.S., except for scant local populations in isolated mountain areas along the border with British Columbia. In northwest Washington, 10–15 grizzlies are estimated to have survived in the North Cascades, with perhaps 35 more in the Selkirk Mountains of northern Washington and adjacent Idaho (O'Gara 1992). Of the coastal populations that descended from the Whidbey Island bear and its contemporaries, none remains alive today.

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Literature Cited

- Carlstad, C. A. 1992. Late Pleistocene deglaciation history at Point Partridge, central Whidbey Island, Washington. M.S. thesis, Western Washington University, Bellingham.
- Churcher, C. S. and Morgan, A. V. 1976. A grizzly bear from the middle Wisconsin of Woodbridge, Ontario. *Can. Jour. Earth Sci.* 13: 341–347.
- Easterbrook, D. J. 1992. Advance and retreat of cordilleran ice sheets in Washington, U.S.A. *Geographie Physique et Quaternaire* 46: 51–68.
- Erdbrink, D. P. 1953. A Review of Fossil and Recent Bears of the Old World. Publicatie Van Het Min. Geologisch Instituut Rijks Universiteit Utrecht, Netherlands.
- Graham, R. W. 1991. Variability in the size of North American black bears (*Ursus americanus*) with the description of a fossil black bear from Bill Neff Cave, Virginia. *Illinois State Museum Sci. Pap.* 23: 238–280.
- Guilday, J. E. 1968. Grizzly bears from eastern North America. *Amer. Midland Naturalist* 79: 247–250.
- Gustafson, C. E., Gilbow, D., and Daugherty, R. D. 1979. The Manis Mastodon site: early man on the Olympic Peninsula. *Can. Jour. Archaeol.* 3: 137–164.
- Harington, C. R., 1975. Pleistocene Muskoxen (*Symbos*) from Alberta and British Columbia. *Can. Jour. Earth Sci.* 23: 903–919.
- . 1989. Pleistocene vertebrate localities in the Yukon: in Carter, L. D., T. D. Hamilton, and J. P. Gallo-way, eds., *Late Cenozoic History of the Interior Basins of Alaska and the Yukon*. U.S. Geol. Surv. Circular 1026: 93–98.

- Heaton, T. H. and Grady, F. 1993. Fossil grizzly bear (*Ursus arctos*) from Prince of Wales Island, Alaska, offer new insights into animal dispersal, interspecific competition, and age of deglaciation. *Current Research in the Pleistocene* 10: 99-100.
- Heusser, C. J. 1977. Quaternary palynology of the Pacific slope of Washington. *Quaternary Research* 8: 282-306.
- Hopkins, D. M. 1967. The Cenozoic history of Beringia—a synthesis, in D. M. Hopkins, ed., *The Bering Land Bridge*, Stanford University Press: 451-484.
- Kurtén, B. 1960. A skull of the grizzly bear (*U. arctos* L.) from Pit 10, Rancho la Brea: Los Angeles County Museum Contrib. Sci. 39:1-7.
- . 1963. Notes on some Pleistocene mammal migrations from the Palaearctic to the Nearctic. *Eiszeitalter u. Gegenwart* 14:96-103.
- . 1968. *Pleistocene Mammals of Europe*. Aldine Publishing Company, Chicago.
- . 1976. *The Cave Bear Story*. Columbia University Press, New York.
- Kurtén, B. and Anderson, E. 1974. Association of *Ursus arctos* and *Arctodus simus* (Mammalia: Ursidae) in the Late Pleistocene of Wyoming. *Brevoria* 426:1-6.
- Lyman, R. L. 1968. On the Holocene history of *Ursus* in eastern Washington. *Northwest Sci.* 60:67-71.
- Mehring, P. J., Jr. 1988. Weapons of ancient Americans. *Nat. Geographic* 174 (4):500-503.
- Mehring, P. J., Jr. and Foit, F. F., Jr. 1990. Volcanic ash dating of the Clovis cache at East Wenatchee, Washington. *Nat. Geographic Res.* 6(4):495-503.
- Merriam, C. H. 1918. Review of the grizzly and big brown bears of North America. *North Amer. Fauna* 41:1-136.
- Miller, G. S., Jr. 1899. A new fossil bear from Ohio. *Proc. Biol. Soc. Wash.* 13:53-56.
- Mundy, K. R. D. and Flook, D. R. 1973. Background for managing grizzly bears in the national parks of Canada. *Can. Wildlife Serv. Rept. Series* 22:7-34.
- Newcomb, R. C. and Repenning, C. A. 1970. Occurrence of mammoth fossils in the Touchet Beds, south-central Washington. *Northwest Sci.* 44:16-18.
- Noe-Nygaard, N. 1983. A new find of Brown Bear (*Ursus arctos*) from Star Carr and other finds in the Late Glacial and Post Glacial of Britain and Denmark. *Jour. Archeol. Sci.* 10:317-325.
- O'Gara, G. 1992. A grizzly's place. *Sierra* 77(5):57-61, 80-84.
- Petersen, K. L., Mehring, P. J., Jr., and Gustafson, C. E. 1983. Late-Glacial vegetation and climate at the Manis Mastodon site, Olympic Peninsula, Washington. *Quaternary Research* 20:215-231.
- Peterson, R. L. 1965. A well-preserved grizzly bear skull recovered from a Late Glacial deposit near Lake Simcoe, Ontario. *Nature* 208: 1233-1234.
- Pielou, E. C. 1991. *After the Ice Age*. University of Chicago Press.
- Rensberger, J. M., Barosky, A. D., and Spencer, P. 1984. Geology and glaciology of a Pleistocene-to-Holocene loess succession, Benton County, Washington. *Archaeological and Historical Services Report* 100-39, Eastern Washington University, Cheney, Washington.
- Rausch, R. L. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylbasal length. *Can. Jour. Zool.* 41:33-45.
- Schultz, J. R. 1938. A Late Quaternary mammal fauna from the tar seeps of McKittrick, California. *Carnegie Inst. Wash. Pub.* 487, Part 4:118-161 + 17 plates.
- Scott, W. F. 1967. A mammoth from the Touchet Beds near Walla Walla, Washington (abstract). *Northwest Sci.* 41:60-61.

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Gregory D. Hayward, USDA Forest Service, Intermountain Forest and Range Experiment Station, 222 South 22nd Street, Laramie, WY 82070¹

and

Patricia H. Hayward, 786 Roger's Canyon Rd, Laramie, WY 82070¹

Relative Abundance and Habitat Associations of Small Mammals in Chamberlain Basin, Central Idaho

Abstract

We sampled small mammal populations and measured habitat structure in forested and non-forested habitats in the wilderness of central Idaho over a 5-year period using pit and snap traps. Although results from pit and snap trapping differed for northern pocket gophers (*Thomomys talpoides*), capture rates for the two methods were similar across habitats for the other common species. Southern red-backed voles (*Clethrionomys gapperi*) and shrews (*Sorex vagrans* and *S. cinereus*) were the most common species captured. Spruce-fir forest exceeded other habitats in the abundance of small mammals while all sites had low species richness ($s = 4-7$). Habitat associations of the common small mammals (southern red-backed voles, shrews, deer mice (*Peromyscus maniculatus*), and yellow-pine chipmunks (*Tamias amoenus*)) differed, based on both broad patterns and microhabitat gradients. Our data corroborate the results of other investigations by demonstrating the relatively low abundance of small mammals in subalpine habitats of the Rocky Mountains. Furthermore the differences in small mammal communities among forest types suggests a mosaic pattern of small mammal communities in the Rockies which results from the patchy nature of forests in this region.

Introduction

Small mammal populations play important roles in subalpine ecosystems. Patterns of succession and species composition of forests may be altered through seed consumption patterns of mice, voles, and chipmunks (e.g. Abbott 1961, Sullivan 1979, Halvorson 1982, Vander Wall 1992). Similarly, dispersion patterns of hypogeous mycorrhizal fungi occurs, in part, from the dispersal of spores by squirrels and voles which feed on the below-ground fruiting bodies (Fogel and Trappe 1978, Maser *et al.* 1978, Ure and Maser 1982). The success of young conifers may depend on whether they successfully form a symbiotic relationship with mycorrhizal fungi (Marks and Kozlowski 1973, cited by Maser *et al.* 1978). In addition to their interaction with primary producers and decomposers, small mammals are essential prey for several subalpine carnivores including boreal owls (*Aegolius funereus*) (Hayward *et al.* 1993), great gray owls (*Strix nebulosa*) (Bull *et al.* 1989), and American marten (*Martes americana*) (Clark *et al.* 1987). Furthermore, small mammals themselves prey upon insects and may influence these taxa (e.g. Johnson 1964, Martell and Macaulay 1981, Merritt 1981).

Despite the important functions of small mammals in subalpine and montane ecosystems, current knowledge does not provide a sound understanding of small mammal distribution and abundance among subalpine habitats in the northern Rocky Mountains. Existing literature provides a limited geographic base and is derived primarily from short-term (1 or 2 year) studies. Two studies have examined small mammal communities in subalpine forests in Wyoming. Raphael (1988) described the abundance and habitat associations of small mammals in subalpine forest based on 3 years of intensive live trapping over 2 watersheds. Brown (1967), during 2 summers, sampled 127 sites in the Medicine Bow mountains including many sites within the subalpine. Over a 3-year span, Millar *et al.* (1985) sampled 102 subalpine sites in Alberta. Williams (1955) examined small mammal communities in montane habitats in Colorado. Several studies have compared small mammal abundance in harvested and unharvested sites in the Rockies (e.g. Campbell and Clark 1980, Halvorson 1982, Medin 1986, Scrivner and Smith 1984, Ramirez and Hornocker 1981).

We collected data on the relative abundance and habitat associations of small mammals in the wilderness of central Idaho. These data complement those of earlier studies by furthering the basis for inferring patterns of species distribution

¹Address during data collection: Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83843

and determining the extent to which patterns are similar among geographic locales. Few studies have examined small mammals from subalpine fir (*Abies lasiocarpa*) forests in Idaho. Furthermore, our study examined a landscape which had not experienced catastrophic disturbance (i.e. stand replacement events) in at least 100 years. The forest stands we sampled were mature and older forest in a landscape where older forest predominates.

Study Area

We examined habitat use by small mammals in the mountains of central Idaho in the northern portion of the 956,515-ha Frank Church, River of No Return Wilderness (RNRW). The study area lay within a ~15,000 ha portion of Chamberlain Basin which extends from 1,580 to 2,194 m elevation on a high, dissected plateau. The entire area is mountainous but lacks steep jagged peaks; few slopes exceed 50%.

Chamberlain Basin lies in the *Abies* life zone and conifer forest covers over 95% of the area (Hayward *et al.* 1993). Lodgepole pine (*Pinus contorta*) dominated the forest, especially in cold-air drainages where monospecific stands of this species covered areas exceeding 300 ha. Lodgepole pine stands generally exceeded 120 years old and some stands included 2 or more age classes of pines. South facing slopes below 1,825 m supported open forest of 60-130 cm diameter-at-breast-height (dbh) ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Limited ring counts suggest that these stands exceeded 250 years since the last stand replacement disturbance. Large woody debris was present on these sites but not abundant. We refer to these forests as mixed-conifer. On cooler aspects up to 2,000 m, Douglas-fir dominated unless fire had produced a lodgepole pine forest. Many of these stands were old forest with several canopy layers, numerous large diameter trees, and some large woody debris. Douglas-fir forests were mixed with subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) up to 2,200 m. Above 2,000 m, spruce-fir forest occupied sites without recent fire.

Meadows and open shrub fields covered <3% of the area. Sagebrush-bunchgrass (*Artemisia* spp.-*Festuca idahoensis*) slopes were the most common open habitat below 1,850 m whereas *Carex* meadows and willow (*Salix* spp.) bogs occurred at

higher elevations. Aspen occurred in small clumps (usually <0.5 ha) below 2,100 m and covered <1% of the landscape.

For the Chamberlain study site, we classified the landscape by dominant overstory vegetation using color 1:5800 aerial photographs. Rank order of landscape coverage from most to least dominant were lodgepole pine, Douglas-fir, spruce-fir, mixed-conifer, meadow and shrub-field openings, and aspen. Lodgepole-pine forest covered over 50% of the Chamberlain study area.

Climate at Chamberlain Basin has a strong Pacific coastal influence during winter but follows continental patterns in summer (Finklin 1988). At 1,700 m elevation, Chamberlain Basin Guard Station receives 76 cm of precipitation per year (50% as snowfall) and snow depths reach 50-90 cm. At 2,150 m, 70% of precipitation is snowfall, and snow depths exceed 150 cm. The frost-free period at 1,700 m lasts 35-40 days. In July, maximum temperatures averaged 28° C with average minimums of 5° C; in February, daily temperature extremes averaged 5° C maximum and -20° C minimum at 1,700 m.

Methods

Small Mammal Trapping

Snap trapping.—Small mammals were sampled at 7 sites using museum special snap traps baited with peanut butter and rolled oats set in a rectangular 9 x 10 grid (90 traps) with 15 m spacing. Traps were checked daily for 7 days. One or 2 grids were trapped at a time so the trapping sequence extended over a 6-week period in the spring. The order of trapping moved from low to high elevation sites so that the phenology of each site was similar at trapping time. Grids were trapped in the same order each year although several grids were added to the study during the 5-year investigation (grids were added as more field help became available during the study and the importance of spruce-fir forest as boreal owl foraging habitat became apparent). The first grid was begun 19 May in 1984 and 1985, 26 May 1986, 22 May 1987, and 23 May 1988.

In 1984, 1 grid was placed in each of 3 vegetation types: sagebrush-bunchgrass, lodgepole-pine forest, and old mixed-conifer forest. In 1985, these sites were trapped in the same order. A wet meadow, a second lodgepole-pine stand, and a mature Douglas-fir forest site were added in 1985

and trapped after previously established sites. All sites trapped in 1985 also were trapped in 1986 plus an additional old spruce-fir stand. These same 7 sites were trapped in 1987. Only the mixed-conifer and Douglas-fir sites were trapped in 1988; we visited our field site for only 2 weeks that spring.

Trap sites were selected subjectively. In selecting specific grid locations we selected sites which: 1) represented the major vegetation types in the study area, 2) were well dispersed throughout the study area, and 3) were relatively large stands of homogeneous vegetation so the trap grid could be placed at least 30 m from an ecotone. Trap sites were well dispersed throughout the study area with some trapping grids separated by over 8 km. Because of the naturally patchy nature of vegetation in Chamberlain Basin large homogeneous blocks of vegetation were not available. Therefore it was not possible to maintain a buffer greater than 30 m between the trapping grid and ecotone at some sites. This was not considered a problem, however, as we sought to examine small mammal populations in this naturally patchy environment.

Pit trapping.—We established 20 pit-trap sites; 18 sites in the summer of 1985 and 2 additional sites in the spring of 1986. All sites were trapped continuously until September 1987. Each pit-trap set consisted of 4 cone-shaped, 40-cm-deep pits placed along a 3-m-long, 15-cm-high, sheet metal, drift fence (Williams and Braun 1983). One pit was located at the ends of the fence and 1 on either side at the center. Each pit was covered with sheet metal held 5 cm above the ground by corner stays. This cover prevented sticks, rain, and snow from entering the pit. Each metal pit contained 8 cm of 50% ethanol topped with mineral oil to preserve captured specimens. Traps were checked once each month from May to August and left functional through the winter.

Sites for pit-trap sets were chosen to distribute the traps throughout the Chamberlain study area and to sample 6 vegetation types: wet meadow, sagebrush-bunchgrass, old mixed-conifer forest, lodgepole pine forest, Douglas-fir forest, and spruce-fir forest. Pit-trap sets sampled 3 stands in each of the 6 vegetation categories, except we placed 5 sets in spruce-fir forest (2 in wet, old-spruce bottoms and 3 in mesic spruce-fir upland).

Vegetation Characterization

We characterized the structure of each forest stand sampled for small mammals and a stratified ran-

dom sample of forest stands throughout the study area. Four cover types (lodgepole pine, spruce-fir, mixed-conifer, and Douglas-fir) together represented over 99% of the forest cover in the study area. In order to quantitatively describe differences in physiognomy among the 4 major forest cover types we chose 22 random points in each of the 4 types from throughout the study area (23 in mixed-conifer by accident) using a random number table and map grid overlay. Stands chosen for small mammal trapping were interspersed among the randomly selected stands. Random sites were assigned to 1 of the 4 types based on overstory species composition. At each site (random and trapping) we measured forest structure to define the physiognomy of the stand.

We quantified forest structure at small mammal trap sites and at random sites (total 101 sites) in a 30-by-75-m plot centered in the small mammal trapping site or random location. Within the sample plot, structure was quantified by density of trees and by percent cover of trees, shrubs, grasses, and forbs. Cover of trees and shrubs was sampled along 4, 30.5-m-parallel transects placed perpendicular to the slope within the plot (Bonham 1989). Transects were randomly spaced 6-30 m apart. Intercept measurements along these transects provided shrub cover estimates (all shrubs were <1 m high) and tree cover estimates in 5 height categories (canopy cover layers) (0-1 m, 1.1-2 m, 2.1-4 m, 4.1-8 m, >8 m) (Bauer 1943, Borman and Buell 1964, Hayward and Garton 1988). We recorded the dominant tree species and number of trees and snags in 6 dbh classes (2.5-7.6 cm, 7.7-15 cm, 15.1-23 cm, 23.1-38 cm, 38.1-53 cm, and >53 cm) within 8 systematically located 83-m² circular plots, 2 per transect (modified from James 1971, Hayward and Garton 1988). Cover of forbs, grasses, and subshrubs (any woody plant species commonly under 15 cm tall) was estimated on 8 0.1 m² rectangular quadrats (Daubenmire 1959), 2 quadrats per transect.

Because the small (83-m²), circular tree plots would underestimate numbers of large diameter trees, variable-radius-plot tree samples were measured from 2 points—1 point along each of transects 2 and 4. We used a relaskop (Spiegel, Inc., Germany) with a 10-factor prism and 30-cm-dbh lower limit to count trees. Densities and basal area were calculated as described by Avery (1975: 170).

Statistical Analysis

Macrohabitat.—Broad habitat associations of small mammal species were examined by comparing the frequency of capture for each species across vegetation types. We examined simple frequency of capture values rather than employing a more complex model because the data did not fit the assumptions of more sophisticated estimators. We treated results from snap-trapping and pit-trapping separately. Neither method can give a completely accurate ranking of species abundance within various habitats. By using both methods we sought to sample a broad range of mammal species and rank the importance of various vegetation types for each species.

Microhabitat.—We examined the microhabitat characteristics of forests used by small mammals within the study area using a principal components analysis (PCA). For this analysis we first developed a forest vegetation ordination based on vegetative structural features measured at both the random locations and the trap locations (101 sites). This analysis included only forest sites because of the problems associated with examining disjunct gradients. For the PCA, we transformed the structural variables to Z scores (Pielou 1984) prior to analysis. This analysis defined the principal component

axes describing primary gradients of the forest habitats of the Chamberlain site.

After examining the ecological pattern of the habitat gradients defined by those principal components with eigenvalues > 1, we compared the forest structure at the 14 forest pit trap sites to the number of mammals captured at each site. To do so, we calculated the Spearman rank correlation between the principal component scores and the abundance of each small mammal species. This analysis excluded pit trap sites in open habitats (wet meadow and sagebrush-bunchgrass). It would have been inappropriate to include these in the PCA because they are not part of the “forest” habitat gradient.

Results

Habitat Use and Relative Abundance

Comparison of sampling methods.—Snap trapping and pit trapping differ in sampling efficiency for different small mammal species (Williams and Braun 1983). We captured a broader array of species in pit traps than snap traps (Tables 1, 2). Pocket gopher (*Thomomys talpoides*), golden-mantled ground squirrel (*Spermophilus lateralis*),

TABLE 1. Number of individuals captured in 9 x 10 snap-trapping grids at 7 sites in Chamberlain Basin, Idaho, during 1984-88. Trap sites are labeled by dominant overstory vegetation. Each grid was run for 7 days during late May or early June for the number of years listed.

	Sage (4 yrs)		Wet meadow (3 yrs)		Lodgepole 1 ^a (4 yrs)		Lodgepole 2 ^b (3 yrs)		Douglas-fir (4 yrs)		Mixed conifer (5 yrs)		Spruce-fir (2 yrs)	
	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
<i>Sorex vagrans</i> and <i>S. cinereus</i>	0 ^c		16		4		1		0		1		71	
<i>Tamias amoenus</i>	18	0	1	0	3	0	4	0	1	0	4	0	0	0
<i>Glaucomys sabrinus</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Peromyscus maniculatus</i>	3	0	0	0	3	0	1	0	7	1	7	3	0	0
<i>Clethrionomys gapperi</i>	0	0	0	0	0	0	1	0	12	0	9	2	66	38
<i>Phenacomys intermedius</i>	0	0	0	0	1	0	0	0	0	1	0	0	1	0
<i>Microtus montanus</i> and <i>M. longicaudus</i>	7	2	5	5	0	0	0	0	0	0	0	0	0	0
<i>Zapus princeps</i>	2	0	1	0	8	0	0	0	0	0	3	0	0	0
Total # individuals per trapping year	8.0		9.3		4.7		3.0		5.5		5.8		88	

^aLodgepole-pine forest with lush understorey vegetation and some downed logs.
^bLodgepole-pine forest with dry understorey and no downed logs.
^cShrews were not aged.

TABLE 2. Relative capture frequency of small mammals sampled using pit traps set year-round at Chamberlain Basin, Idaho, during 1985-88 in 7 vegetation types defined by dominant overstory. Values represent number of captures per 1000 trap-site nights. Three sites were trapped for each vegetation type except spruce bottom, where only 2 sites were trapped. Trap-site days in thousands are recorded in parenthesis. Variation in abundance across vegetation types is represented by the coefficient of variation (Zar 1974) which was calculated after standardizing capture frequency by trapping effort (capture frequency/effort).

Small mammal species	Sage (2.9)	Wet meadow (2.8)	Lodgepole (3.3)	Mixed conifer (3.3)	Douglas-fir (3.0)	Spruce bottom (2.3)	Spruce-fir (2.4)	Coefficient of variation
<i>Sorex vagrans</i> and <i>S. cinereus</i>	8.6	16.1	5.8	8.5	5.3	33.5	18.7	0.88
<i>Sorex palustris</i>	0	0.4	0	0	0	0	0	2.5
<i>Tamias amoenus</i>	2.1	0	2.7	5.5	2.0	0	0	1.11
<i>Spermophilus lateralis</i>	0	0	0	0.9	0	0	0	3.33
<i>Tamiasciurus hudsonicus</i>	0	0	0	0.3	0	0	0	3.0
<i>Glaucomys sabrinus</i>	0	0	0	0	0	0.4	0	3.0
<i>Thomomys talpoides</i>	1.4	1.1	1.5	0	0.3	0	0.4	0.91
<i>Peromyscus maniculatus</i>	3.8	0	1.5	3.0	0.7	2.2	1.2	0.74
<i>Clethrionomys gapperi</i>	0	0	2.7	1.5	8.3	13.9	21.7	1.29
<i>Phenacomys intermedius</i>	0	0	0.6	0.3	0	0	1.2	1.63
<i>Microtus montanus</i> and <i>M. longicaudus</i>	7.9	1.8	0	0	0	0	0.8	1.90
<i>Zapus princeps</i>	1.4	0.4	0.3	0	0	0.4	0	1.42
<i>Mustela erminea</i>	0	0	0	0	0	0.4	0	3.0
Total per 1000 trap nights	8.7	7.1	4.6	6.1	5.5	22.1	18.3	

red squirrel (*Tamiasciurus hudsonicus*), weasel (*Mustela erminea*), and water shrew (*Sorex palustris*) were captured in pit-traps but not snap traps. For each of these species except pocket gophers, however, only 1 to 3 individuals were captured during the entire study. Because of the size of the traps employed and because our traps were not placed in trees, neither trapping method was expected to efficiently sample mammals over ~150 g or arboreal species.

Considering terrestrial mammals less than 150 g, the pocket gopher was the species most differentially sampled by the 2 methods. Pit traps captured pocket gophers on 5 sites, whereas snap traps did not capture this species. For the 3 most frequently captured species, however, pit and snap trapping yielded similar results. Southern red-backed voles (*Clethrionomys gapperi*), shrews (*Sorex vagrans* and *S. cinereus*), and deer mice (*Peromyscus manicula-*

tus) were the most frequently captured species by both methods (Tables 1, 2). To compare the 2 trapping methods, we examined capture rates (frequency of capture) for these 3 small mammals across vegetation types. Capture rates of southern red-backed voles in pit and snap traps were strongly related (Spearman rank correlation, $r_s = 0.94$). The 2 trapping methods also resulted in similar ranking for shrew abundance ($r_s = 0.75$). Capture rate for deer mice differed ($r_s < 0.10$) mainly because pit traps in Douglas-fir forests captured few mice, whereas the number of snap-trapped mice was highest for this habitat. Otherwise the rank order of the habitats was similar for snap and pit-trap samples of deer mice. Based on these results we concluded that the pattern of habitat use illustrated by the snap and pit trapping data represent real ecological patterns and not patterns driven by capture bias of the sampling methods.

Throughout the remainder of the paper we will not consider golden-mantled ground squirrels, red squirrels, flying squirrels (*Glaucomys sabrinus*), or weasels because neither sampling method is designed to effectively sample these species.

Relative abundance of small mammals.—Southern red-backed voles and shrews dominated the small mammal community at Chamberlain (Tables 1, 2). Numbers of shrews and southern red-backed voles captured in pit traps and snap traps were each at least 3 times the number of other small mammal species. The numbers of deer mice, *Microtus* spp., western jumping mice (*Zapus princeps*), yellow-pine chipmunks (*Tamias amoenus*), and pocket gophers were each similar in magnitude.

The number of small mammals captured (lumping all species) was greater in spruce-fir forest than other habitats. Number of individuals captured in spruce-fir forest was nearly double that of all other vegetation types. Fewer individuals were captured in lodgepole pine forest than other habitats (Tables 1, 2).

Broad scale habitat associations.—We combined *Sorex vagrans* and *S. cinereus* for discussion of distribution and abundance because a high proportion of shrews were not identified to species. In general, however, *S. vagrans* was more common in non-forested habitat while *S. cinereus* was the more common shrew in the spruce-fir forests. We captured shrews at all pit-trap sites, and variation in capture rates among habitats was low compared to other small mammals (Table 2). Shrews were more abundant in spruce-fir forests than other vegetation types. Based on pit-trap samples, shrews dominated the small mammal communities in lodgepole pine, mixed-conifer, and unforested habitats.

A water shrew was captured with a pit trap on a single site in a wet meadow. This site was inundated for several weeks each spring and was located within 50 m of a small perennial stream.

We found yellow-pine chipmunks in all habitats except spruce-fir bottoms and spruce-fir uplands. Chipmunks were only captured once at a wet meadow site (snap trapping). Capture rates were the highest in the drier habitats—sagebrush-bunchgrass (snap trapping) and mixed-conifer (pit trapping).

Pocket gophers were caught in all habitats except mixed-conifer and spruce bottoms. Dirt

mounds and “soil ropes” seen throughout the study area suggested that pocket gophers used all but the most rocky habitats. Pit-trap capture rates of pocket gophers were highest in lodgepole pine forest and sagebrush-bunchgrass habitats.

We captured deer mice in all vegetation types except wet meadow. Pit and snap-trap samples differed, however, in the rank order of deer mice captures across habitats. In pit-trap samples, deer mice were most frequently captured in sagebrush-bunchgrass habitats where they were the most frequently captured mammal. Deer mice were also frequently captured in mixed-conifer by pit traps, but rarely in Douglas-fir. Snap-trapping results showed Douglas-fir as the most important habitat for deer mice followed by mixed-conifer, lodgepole, and sagebrush-bunchgrass. During 2 years of snap trapping in the spruce-fir grid, no deer mice were captured.

Southern red-backed voles occurred in all forested vegetation types but capture rates were low in lodgepole pine and mixed-conifer forest. The species was absent from nonforested sites. In both spruce-fir and Douglas-fir forests the biomass of southern red-backed vole captures exceeded that of other small mammals. Southern red-backed voles were captured in both pit and snap traps more frequently in spruce-fir forest than in other types (Tables 1, 2). Average pit-trap capture rates across all years and sites were 2.2 times greater in upland spruce-fir than other types. Snap trapping indicated even larger differences in red-backed vole abundance between spruce-fir and other types; average snap trap capture rates in spruce-fir exceeded all other forests by an order of magnitude.

Heather voles (*Phenacomys intermedius*) were rarely captured (8 individuals in pit and snap traps combined), yet they were found in all forested vegetation types. No more than 3 individuals were captured at any single trap site (a single upland spruce-fir pit trap set); only a single individual was captured at other sites. These voles did not occur in any of the non-forested types.

Montane voles (*Microtus montanus*) and long-tailed voles (*M. longicaudus*) used narrower ranges of habitat than other common small mammal species. In both the pit and the snap traps, we caught *Microtus* spp. in non-forested habitats and a single spruce-fir upland site (Tables 1, 2). *Microtus* capture rates were higher at sagebrush-bunchgrass

sites where *M. longicaudus* was more frequent than in wet meadow where *M. montanus* was most common.

Western jumping mice were found in all habitats except Douglas-fir forest. Despite their relative scarcity across habitats, jumping mice were the most frequently captured species in 1 lodgepole pine site (Table 1). Traps within lodgepole pine where jumping mice were captured generally occurred near wet areas with lush understory vegetation.

Species richness among vegetation types.—We examined species richness among vegetation types using pit trap results (excluding golden-mantled ground squirrels, red squirrels, flying squirrels, or weasels). For this comparison we used pit trap results because this method sampled a wider range of small mammals (e.g. pocket gophers). In decreasing order, species richness was, lodgepole pine (7 species), spruce-fir upland (6), mixed-conifer (6), sagebrush-bunchgrass (6), Douglas-fir (5), wet-meadow (5), and spruce bottom (4).

Microhabitat Associations

In the preceding section we described broad habitat associations of small mammals. Below we will examine further the relationships between forest structure and small mammal capture rates.

Based on analysis of vegetation measurements from 101 forest sites we identified 6 predominant structural gradients of forest habitats available at Chamberlain. The predominant structural gradients were defined by PCA (Table 3). From 21 simple structural variables, PCA defined 6 components with eigenvalues > 1 , accounting for 75% of the overall variance. The seventh component accounted for less variance (4.75%) than would be expected for any one of the original variables.

We interpreted the principal components as follows:

1. Component 1 describes a complex gradient from highly structured, mature and older forest with many canopy layers to young or aggradation

TABLE 3. Six principal components derived from analysis of structural features measured at 101 plots in 4 forest vegetation types at Chamberlain Basin, Idaho, in 1985. Zero loading was 0.45 throughout.

Structural feature	Principal component					
	1	2	3	4	5	6
Basal area	0.668	-0.452	0.478			
Density trees 2.5-7.6-cm dbh		0.687				
Density trees 7.7-15-cm dbh	-0.733	0.481				
Density trees 15.1-23-cm dbh	-0.513			0.501		
Density trees 23.1-38-cm dbh				0.722		
Density trees 38.1-53-cm dbh	0.553					
Density trees > 53 -cm dbh	0.514	-0.487	0.477			
Density snags 2.5-38-cm dbh	-0.767					
Density snags > 38 -cm dbh					0.588	
Conifer cover 0-1 m	0.544	0.634				
Conifer cover 1.1-2 m	0.666	0.607				
Conifer cover 2.1-4 m	0.763					
Conifer cover 4.1-8 m	0.596					
Conifer cover > 8 m			0.720	0.480		
Horizontal cover diversity	0.812					
Low conifer vertical diversity	0.605	0.745				
High conifer vertical diversity	-0.479		0.604			
Subshrub cover		0.467				
Grass cover					-0.555	
Forb cover						0.685
Eigenvalue	5.839	3.771	2.037	1.743	1.223	1.104
% variance explained	27.8	18.0	9.7	8.3	6.1	5.3
Cumulative %	27.8	45.8	55.5	63.8	69.9	75.2

stage forest with little vertical diversity. This component describes the overall physiognomy of the stand whereas subsequent components relate to individual features of forest structure (i.e., understory, overstory).

2. Component 2 defines a gradient with dense cover 0-2 m above the ground, numerous 2.5 to 15-cm-dbh trees and few large trees describing the positive end.

3. Component 3 defines a cline in occurrence of large trees (> 53 cm dbh), high basal area, and upper canopy cover.

4. Component 4 defines a gradient in trees 15.1-38-cm dbh with a well developed upper canopy.

5. Component 5 describes a gradient with large snags (> 38 cm dbh) and little grass cover on the positive end of the gradient.

6. Component 6 is a gradient in forb ground cover.

Using the first 6 principal components we compared forest structures measured at 14 forest pit trap sites to the number of mammals captured at each site. Spearman rank correlation between principal component scores and capture rate for 4 small mammal species suggested differences in habitat use (we considered $P < 0.10$ as sufficient evidence to suggest a relationship and $P < 0.05$ as strong evidence). In this analysis, we considered only those small mammal species captured in at least half the 14 forested pit trap sites.

Southern red-backed vole capture rates were positively related to complexity of forest structure (PC1) (Spearman Rank Correlation ($r_s = 0.61$, $P = 0.02$) but not related to other gradients (Table 4). Shrews appeared to respond positively to increased forest complexity, increasing number of canopy layers, forest age (PC1), and to sites with-

out heavy grass cover but with large diameter snags (PC5). The presence of a complete upper forest canopy cover or high density of 15-38 cm dbh trees appeared associated with reduced shrew capture rate (PC4).

Deer mouse capture rate was not significantly correlated with any of the principal components suggesting that the mice responded to factors unrelated to the forest structure characteristics we measured or were simply ubiquitous in these forest habitats. The response of chipmunks to habitat structure contrasted with the other small mammals examined. The sign of correlations between chipmunks and principal components were opposite those of southern red-backed voles and shrews. Chipmunk captures were especially less numerous in forest with complex structure, high vertical diversity, and many large trees, or forests with dense cover 0-2 m above the ground (PC1 and PC2).

Discussion

Relative Abundance

Fifteen species of mammals were captured in pit or snap traps in Chamberlain basin but a majority of species were not common. Only shrews and southern red-backed voles were common and even these species were only common in spruce-fir forests.

Few studies of small mammals in subalpine forests in the Rocky Mountains have used trap grids or pit trapping comparable to ours. Williams (1955), Brown (1967), Campbell and Clark (1980), Ramirez and Hornocker (1981), and Millar *et al.* (1985) trapped with 1-3 transects rather than in a grid. Halvorson (1982) and Scrivner and Smith (1984) provide the most comparable studies from this region. Their results suggest that the

TABLE 4. Relationships (Spearman Rank Correlation) between small mammal capture rate and forest structure measured at 14 pit-trap sites. Forest structure was defined by principal component scores describing six gradients of forest structure from analysis of 101 forest sites including the 14 trapping locations. Significant correlations are highlighted (* $P \leq 0.10$, ** $P \leq 0.05$).

Species	Principal Component					
	1	2	3	4	5	6
<i>Clethrionomys gapperi</i>	0.61**	0.38	0.08	-0.14	0.45	0.06
<i>Sorex vagrans</i> and <i>S. cinereus</i>	0.55**	0.11	-0.10	-0.49*	0.79**	0.18
<i>Peromyscus maniculatus</i>	-0.01	0.12	-0.18	-0.50	0.18	-0.24
<i>Tamias amoenus</i>	-0.58**	-0.68**	0.21	0.24	-0.36	0.01

abundance of voles on the spruce-fir snap-trap grid at Chamberlain are similar to other sites studied in the Rockies. On our most productive snap-trap grid (an old spruce-fir forest), we caught an average of 8.3 red-backed voles/100 trap nights during a week of trapping each spring for 2 years. Halvorson (1982) captured an average of 8.5 and 6.1 voles/100 trap nights on 2 timbered plots in Montana. Scrivner and Smith (1984) captured an average of 2.9 voles/100 station nights (they had 2 traps per station) on their old forest site in Area 1 and 0.7/100 station nights at the old forest site in Area 2 (Areas 1 and 2 were different study areas).

Neither Halvorson (1982) or Scrivner and Smith (1984) report capturing shrews. In both studies, however, more deer mice were captured than on any of the snap-trap grids at Chamberlain. On our Douglas-fir snap-trap grid we captured 0.3 deer mice/100 trap nights; more than on any other site. Halvorson (1982) reported an average of 1.8 and 2.3 deer mice/100 trap nights on 2 timbered plots. In Idaho mature grand-fir (*Abies grandis*) forest, Scrivner and Smith (1984) captured an average of 12.9 deer mice/100 station nights in Area 1, and 7.4/100 station nights in Area 2.

Raphael's (1988) study in subalpine forest in Wyoming produced a very similar list of species and relative abundance's as we found in Idaho despite the difference in methods (the Wyoming study placed trap stations 200 m apart along ~1.4 km transects in a large grid). In Wyoming, the rank order of small mammal captures across all sites was: southern red-backed vole, shrews (*Sorex cinereus*, *S. monticolus*, *S. hoyi* and *S. nanus*), deer mouse, chipmunks (*Tamias minimus* and *Tamias umbrinus*), western jumping mouse, voles (*Microtus montanus*, *M. longicaudus*), heather vole, golden-mantled ground squirrel, water shrew, weasel (*Mustela erminea*), northern pocket gopher, and house mouse (*Mus musculus*). Red squirrels were common in both Idaho and Wyoming but not sampled comparably. The species of shrews and chipmunks differed between Idaho and Wyoming and northern flying squirrels were absent from Wyoming. Otherwise, the rare occurrence of northern pocket gophers in the Wyoming sample is the most striking difference between our results and Raphael's (see Table 2).

Habitat Associations

Common species of small mammals at Chamberlain displayed relatively strong habitat associations

at either a macro- or microhabitat scale. Furthermore, despite broad overlap among species in habitats used, there were differences in the habitat where species were most common. *Microtus* voles were virtually confined to non-forested sites while southern red-backed voles and heather voles were not trapped in meadow or shrub habitats.

Southern red-backed voles and shrews were far more abundant in spruce-fir forest than any other habitat. These results corroborate patterns observed in other geographic areas (e.g. Raphael 1988, Ramirez and Hornocker 1981, Brown 1967, Millar *et al.* 1985). Others have suggested that red-backed voles are associated with characteristics of mesic, mature forests as a consequence of their food habits and need for moisture (Maser *et al.* 1978, Ure and Maser 1982). Microhabitat analysis for the red-backed voles at Chamberlain indicated an association with complex, mature forest structure which produce the lichen and fungi which this species feeds upon.

Deer mice occurred in all habitats except wet meadows. Other investigations in the Rocky Mountains have demonstrated the wide range of habitats used by this species (e.g. Williams 1955, Brown 1967, Halvorson 1982). This species' greater abundance in drier habitats—sagebrush-bunchgrass, mixed-conifer, and Douglas-fir—may be associated with the production of seeds by grasses and forbs which occur in these habitats. Although deer mice were captured in spruce-fir pit traps, these mice were not captured on the spruce-fir, snap-trap-grid during 2 years of trapping.

Heather voles were trapped in all forested habitats but were always rare. The pattern of broad habitat association (in some cases including non-forested sites) but low capture rates, seems to characterize this species in the Rocky Mountains (Millar *et al.* 1985, Brown 1967, Williams 1955). In contrast, high densities of heather voles have been found in jack pine monocultures with heavy ground cover of Ericaceous shrubs (Foster 1961, Naylor *et al.* 1985). The life history of this species is not understood, however, further study of heather vole demography and life history strategy could provide insight into mechanisms for persistence in small populations.

Yellow-pine chipmunks differed from red-backed voles, shrews and deer mice in their relation to microhabitat gradients. This species also differed from other small mammals in macrohabitat associations. Chipmunks were the most common mammal in sagebrush-bunchgrass sites (snap

trapping) but were also common in dry forest habitats (lodgepole pine and mixed-conifer).

Differences in species' habitat associations led to substantial differences in the structure of small mammal communities across vegetation types. Although lodgepole pine forest had the highest species richness (7) it had the fewest individuals captured in the snap trap sample. Furthermore, abundance of each species was quite similar in lodgepole pine. Mixed-conifer and Douglas-fir forests had similar species richness, abundance of individuals, and (based on both pit and snap trapping) similar mix of species. Wet meadow, which had a low species richness, differed most from the other sites in species composition. Spruce-fir forest stood out from other habitats in the abundance of small mammals and the degree of dominance of the community by shrews and red-backed voles. On the spruce-fir snap-trapping-grid, over 99% of all captures were shrews and red-backed voles. No other habitat was dominated by two species to this extent.

Conclusions

Our data corroborate the results of other investigations by demonstrating the relatively low abundance of small mammals in subalpine habitats of the Rocky Mountains. The abundance of mice and voles at Chamberlain paralleled pattern observed elsewhere in the Rockies but was low compared to studies in Scandinavia. The trapping rate at our most productive site was less than snap trap capture rates reported by Lofgren *et al.* (1986) and Korpimäki (1987a,b) during vole peaks during their studies of boreal owls in Sweden and Finland. Lofgren *et al.* (1986) captured 16.6 voles/100 trap nights during vole peaks and 1.4 during low years. Similarly, Korpimäki (1987a,b) captured up to 18 voles/100 trap nights in Finland during peak vole years. During all years, our trapping rates in habitats other than spruce-fir were lower than those observed by Lofgren *et al.* (1986) during low prey years.

Differences we observed in small mammals (e.g. species composition, species richness) among habitats suggests a mosaic pattern of small mammal communities in the Rockies. Subalpine forests in this region occur in a mosaic or patchwork of successional stages and species associations (Peet

1988, Knight 1994). Patches of lodgepole pine in various stages of succession are mixed among patches of spruce-fir forest. Patch sizes are generally small (10's to 100's of ha) leading to patchiness at the watershed scale. The relationship of small mammals with habitat conditions, then, results in frequent changes in small mammal communities within landscape areas less than 1000 ha.

The landscape mosaic of small mammal communities likely influences higher trophic levels. Many species of carnivores that occur in subalpine habitats are food limited and prey primarily on small mammals (e.g. boreal owls—Lofgren *et al.* 1986, Korpimäki 1987a; great gray owls—Duncan and Hayward 1994; American marten—Thompson and Colgan 1987). The value of each subalpine patch as foraging habitat for these carnivores will be determined, in part, by the small mammal community. Foraging habitat use, daily movement patterns, and population parameters of these carnivores may be effected by the landscape pattern of the small mammal communities.

Finally, variation in the species composition and structure of small mammal communities likely result in different consequences for the plant community in which they occur. While red-back voles frequently feed on *Bryoria* lichen and fungal sporocarps (Martell 1981), deer mice consume seeds, berries and insects (Martell and Macaulay 1981), and pocket gophers kill many conifer seedlings by consuming both above and below-ground parts (Crouch 1971). As the species composition of small mammal communities change among habitats the mammals will differentially effect the dominant overstory as well as understory.

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Literature Cited

- Avery, T. E. 1975. Natural resource measurements. McGraw Hill Book Co., Inc., New York, N.Y. 339pp.
- Abbott, H. G. 1961. White pine seed consumption by small mammals. *J. Forestry* 59:197-201.
- Bauer, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. *Ecology* 24:45-60.
- Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley & Sons, Inc., New York, N.Y. 338pp.
- Borman, F. H., and M. F. Buell. 1964. Old-age stand of hemlock-northern hardwood forest in central Vermont. *Bull. Torrey Bot. Club* 91:451-465.
- Brown, L. N. 1967. Ecological distribution of mice in the Medicine Bow Mountains of Wyoming. *Ecology* 48:677-680.
- Bull, E. L., M. G. Henjum, and R. S. Rohweder. 1989. Diet and optimal foraging of great grey owls. *J. Wildl. Manage.* 53:47-50.
- Campbell, T. M. and T. W. Clark. 1980. Short-term effects of logging on red-backed voles and deer mice. *Great Basin Naturalist* 40:183-189.
- Clark, T. W., E. Anderson, C. Douglas, and J. Strickland. 1987. *Martes americana*. *Mammalian Species* 289:1-8.
- Crouch, G. L. 1971. Susceptibility of ponderosa, jeffrey and lodgepole pines to pocket gophers. *Northwest Sci.* 45:252-256.
- Daubenmire, R. F. 1959. A canopy-coverage method of vegetation analysis. *Northwest Sci.* 33:43-46.
- Duncan, J. R. and P. H. Hayward. 1994. Review of technical knowledge: Great gray owl. pages 159-175. in: G. D. Hayward and J. Verner. eds. *Flammulated, boreal, and great gray owls in the United States: A technical conservation assessment*. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-253.
- Finklin, A. I. 1988. Climate of the Frank Church, River of No Return Wilderness, Central Idaho. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-240. 221pp.
- Fogel, R., and J. M. Trappe. 1978. Fungus consumption (*Mycophagy*) by small animals. *Northwest Sci.* 52:1-31.
- Foster, J. B. 1961. Life history of the phenacomys vole. *J. Mammalogy* 42:181-198.
- Halvorson, C. H. 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. *Ecology* 63:423-433.
- Hayward, G. D., and E. O. Garton. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* (Berlin) 75:253-265.
- Hayward, G. D., P. H. Hayward, and E. O. Garton. 1993. *Ecology of Boreal Owls in the northern Rocky Mountains, USA*. *Wildlife Monographs* 124:159.
- James, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-236.
- Johnson, D. R. 1964. Effects of range treatment with 2,4-D on food habits of rodents. *Ecology* 45:241-249.
- Knight, D. H. 1994. Dynamics of subalpine forests. pages 128-138. in: G. D. Hayward and J. Verner. eds. *Flammulated, boreal, and great gray owls in the United States: A technical conservation assessment*. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-253.
- Korpimäki, E. 1987a. Clutch size, breeding success and brood size experiments in Tengmalm's owl *Aegolius funereus*: a test of hypothesis. *Ornis Scand.* 18:277-284.
- . 1987b. Selection for nest hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. *J. Anim. Ecol.* 56:185-196.
- Lofgren, O., B. Hornfeldt, and B. G. Carlsson. 1986. Site tenacity and nomadism in Tengmalm's owl (*Aegolius funereus* (L.)) in relation to cyclic food production. *Oecologia* (Berlin) 69:321-326.
- Marks, G. C., and T. T. Kozlowski. 1973. *Ectomycorrhizae: their ecology and physiology*. Academic Press, New York, N. Y.
- Martell, A. M. 1981. Food habits of southern red-backed voles (*Clethrionomys gapperi*) in northern Ontario. *Can. Field Naturalist* 95:325-328.
- Martell, A. M., and A. L. Macaulay. 1981. Food habits of deer mice (*Peromyscus maniculatus*) in northern Ontario. *Can. Field Naturalist* 95:319-324.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* 59:779-809.
- Medin, D. E. 1986. Small mammal responses to diameter-cut logging in an Idaho Douglas-fir forest. U. S. D. A. For. Serv. Research Note INT-362. 6pp.
- Merritt, J. F. 1981. *Clethrionomys gapperi*. *Mammalian Species* 146:1-9.
- Millar, J. S., G. L. Duncan, and V. A. Loewen. 1985. Habitat use by non-hibernating small mammals of the Kananaskis Valley, Alberta. *Canadian Field-Naturalist* 99:196-204.
- Naylor, B. J., J. F. Bendell, and S. Spire. 1985. High density of heather voles, *Phenacomys intermedius*, in jack pine, *Pinus banksiana*, forests in Ontario. *Canadian Field Naturalist* 99:494-497.
- Peet, R. K. 1988. Forests of the Rocky Mountains. pages 63-101. in: M. G. Barbour and W. D. Billings, eds. *North American terrestrial vegetation*. Cambridge Univ. Press, Cambridge, England.
- Pielou, E. C. 1984. The interpretation of ecological data: a primer on classification and ordination. John Wiley & Sons, Inc., New York, N.Y. 263 pp.
- Raphael, M. G. 1988. Habitat associations of small mammals in a subalpine forest, Southeastern Wyoming. pages 359-367. in: R. C. Szaro, K. E. Severson, and D. R. Patton eds. *Management of amphibians, reptiles, and small mammals in North America*. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-166.
- Ramirez, P. and M. Hornocker. 1981. Small mammal populations in different-aged clearcuts in Northwestern Montana. *J. Mamm.* 62:400-403.
- Scrivner, J. H. and H. D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce-fir forest in Idaho. *Northwest Sci.* 58:171-176.
- Sullivan, T. P. 1979. Repopulation of clear-cut habitat and conifer seed predation by deer mice. *J. Wildl. Manage.* 43:861-871.
- Thompson, I. D. and P. W. Colgan. 1987. Numerical responses of martens to a food shortage in north central Ontario. *J. Wildl. Manage.* 51:824-835.
- Ure, D. C., and C. Maser. 1982. *Mycophagy of red-backed voles in Oregon and Washington*. *Can. J. Zool.* 60:3307-3315.
- Vander Wall, S. B. 1992. The role of animals in dispersing a "wind-dispersed" pine. *Ecology* 73:614-621.

- Williams, O. 1955. Distribution of mice and shrews in Colorado montane forest. *J. Mamm.* 36:221-231.
- Williams, D. F., and S. E. Braun. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. *J. Wildl. Manage.* 47:841-845.
- Zar, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, N.J. 620 pp.

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Influence of Temperature on Incubation Rates of Coho Salmon (*Oncorhynchus kisutch*) from Ten Washington Populations

Abstract

Coho salmon embryos from 10 Washington populations were incubated under controlled conditions to determine the levels of variation in time to hatch among populations and families within populations. The average incubation rate was somewhat slower than that estimated from a quantitative model derived from British Columbia populations, and was slightly faster than that predicted by a Washington model. Significant variation in incubation rates among the Washington populations was detected, consistent with results from other studies. Dates of first hatching of families within populations ranged more than two weeks at 6°C. Within families, the first and last individuals to hatch ranged over 1-3 weeks. The variation in incubation rate among populations likely reflects local adaptation to the thermal regimes of the rivers. The variation within populations and families will contribute to the variation in emergence date of fry, which will affect their growth and survival.

Introduction

Water temperatures in streams are chiefly influenced by local air temperature, shade, stream depth and groundwater inputs (Sullivan *et al.* 1990). Although stream temperatures are naturally dynamic, human activities such as timber removal can alter thermal regimes (Holtby 1988, Thedinga *et al.* 1989). Recent physico-geomorphic models (Sullivan *et al.* 1990) can forecast the effects of such human activities on stream temperatures but the biological consequences of temperature changes on stream fishes are imperfectly understood. Wide-spread landscape alterations in the Pacific Northwest have generated concern over the status of fishes in general and Pacific salmon (*Oncorhynchus* spp.) in particular (Nehlsen *et al.* 1991).

Temperature regimes are a major factor contributing to the local adaptation and isolation of salmon populations (Ricker 1972, Murray *et al.* 1990). Temperatures directly affect the rate of embryonic development, hatch rates, survival and size of embryos (Tang *et al.* 1987, Beacham and Murray 1990, Murray *et al.* 1990). The time of year when adults spawn also is related to the temperature regime that the embryos will experience and the period of peak food abundance in spring (Godin 1982, Beacham and Murray 1987, Brannon 1987). Increased incubation temperature can result in early emergence, longer growing season, larger size and higher over-winter survival rates of stream-resident species such as coho salmon, *O. kisutch* (Holtby 1988), but they also can lead to a mis-match between the timing of downstream

migration and adequate levels of marine food resources, leading to reduced marine survival (Holtby 1988, Holtby and Scrivener 1989).

Species-specific models (e.g., Beacham and Murray 1990) have been developed to project hatch times and developmental stage of salmon embryos, given a known or simulated temperature regime (e.g., Sullivan *et al.* 1990). These projections can aid in assessing potential consequences of early emergence (Holtby 1988), physical disturbance in streams (Johnson *et al.* 1989), or dewatering of streams (Graybill *et al.* 1979, Becker *et al.* 1983) on developing salmon. However, the variation in temperature among streams and the tendency of salmon populations to evolve local adaptations (Ricker 1972, Taylor 1991) indicates that species-specific models must be used with caution, as populations may vary considerably in time to hatch (Brannon 1987, Beacham and Murray 1989). Most of the information on incubation rate has been reported for populations of salmon in B.C. (e.g., sockeye: Brannon 1987, chinook, pink and chum: Beacham and Murray 1989, 1986, 1987, coho: Murray *et al.* 1990).

The purpose of this study was to examine the amount of variation in time to hatch among and within populations of coho salmon in Washington state. Coho salmon were selected because: (1) altered incubation temperatures may affect subsequent life-history events (Holtby 1988); (2) many populations in Washington (Washington Department of Fisheries *et al.* 1993) and Oregon (Nickelson *et al.* 1992) are in jeopardy; and (3) the British Columbia data may not be representative of populations in Washington. Specifically, we

examined variation in incubation rate under different temperature regimes among populations, among families within populations, and among individuals within families.

Materials and Methods

Gametes from 10 coho salmon populations in Washington were collected in fall and winter of 1989-1992 (Figure 1). Fish representing both the early and late spawning run of coho in the Solduc River were also sampled in 1990. Gametes were transported to either the University of Washington hatchery facility in Seattle or the University's research facility located at Big Beef Creek, Seabeck, Washington. In 1989, one female from each river was crossed with one male to form a single full sibling cross. This provided general information of the variance of individual hatch rates about the true mean of a single family.

The females collected in 1990-91 were each mated with two males from their respective populations to form half sibling crosses. Usually this type of cross is made and replicated to allow statistical partitioning of the paternal, maternal, and interactive genotypic effects on the phenotype, in this case, time to hatch. Due to hatchery space constraints, crosses were not replicated, thus rigorous statistical treatment of the genotypic data was not possible.

The 1989 and 1990 crosses were each divided into four lots of approximately 250 eggs. Embryos were incubated at 6, 8, 10, and 13°C ($\pm 0.5^\circ$) in 1989 and at 6, 9, and 12°C ($\pm 0.5^\circ$) in 1990. Embryos were incubated in polyvinyl chloride (PVC) cups (7.6 cm diameter and 6.4 cm high) with plastic mesh bottoms. Ten cups were placed centrally on plastic grids approximately 7 cm above the incubation trough (1.0 x 0.5 x 0.15 m) floor. A 2.5 cm dia. x 0.5 m long perforated PVC pipe was installed at the head of the trough to evenly distribute flows (8 l min⁻¹). Dechlorinated municipal water was chilled by an immersion-coil cooler or warmed by a steam heat exchanger. The 1991 crosses were divided into lots of approximately 500 and each lot was individually incubated (6°C $\pm$ 0.3) in a vertically stacked Heath tray.

Embryos were checked every two days to monitor hatch rates and remove dead eggs and alevins. Days and thermal units or TUs (°C x number of incubation days) to different hatching stages were noted for all crosses. Dissolved oxygen levels were

monitored in the troughs and Heath trays and were consistently at or near saturation. Temperatures were controlled automatically, and continuously recorded electronically. Embryos were incubated in total darkness except when light was needed to monitor hatching.

Results

Single crosses (one female crossed with one male) from the Toutle, Elochoman, Baker and Clark rivers were incubated at 6, 8, 10 and 13°C in 1989. The number of TUs required to obtain 50% hatching of Toutle River embryos increased with increasing temperature (Figure 2). Elochoman and Baker River eggs required slightly fewer TUs to 50% hatch at the lower and higher (6° and 13°) than at intermediate temperatures (Figure 2). Clark Creek embryos required slightly more TUs to 50% hatch at 6°C than embryos from the other rivers and 100% mortality was observed in the 13°C treatment. The number of TUs required from first to 50% hatch decreased with increasing temperature for all families. For example, Elochoman River eggs required 138 TUs from first to 50% hatch at 6°C, and only 39 TUs at 13°C.

Five populations (represented by 2-6 families per population) incubated at 6, 9 and 12°C (Table 1) exhibited considerable variation in incubation rate at a given temperature. For example, embryos from the Toutle, Snow and Cowlitz rivers required, on average, more TUs to 50% hatch at 9°C than at 6°C, whereas embryos from the early and late runs of the Solduc River required the same or fewer. Embryos collected after 27 November (Solduc-late run, Snow, and Cowlitz rivers) required fewer TUs to reach 50% hatch than embryos collected on 30 October from the Solduc early run. The Toutle River embryos, collected 1 November, had similar 50% TU requirements to the later spawning populations at 6 and 12°C, but required more TUs to 50% hatch at 9°C than the other populations. The Toutle River incubation rates were the least protracted at 6 and 12°C and the most protracted at 9°C, relative to all other populations.

We compared incubation rates of embryos collected from the early (30 October 1990) and late (27 November 1990) spawning runs of coho in the Solduc River (Table 1). The early run embryos incubated at 6°C required, on average, 135 more TUs to realize first hatch and an additional 135

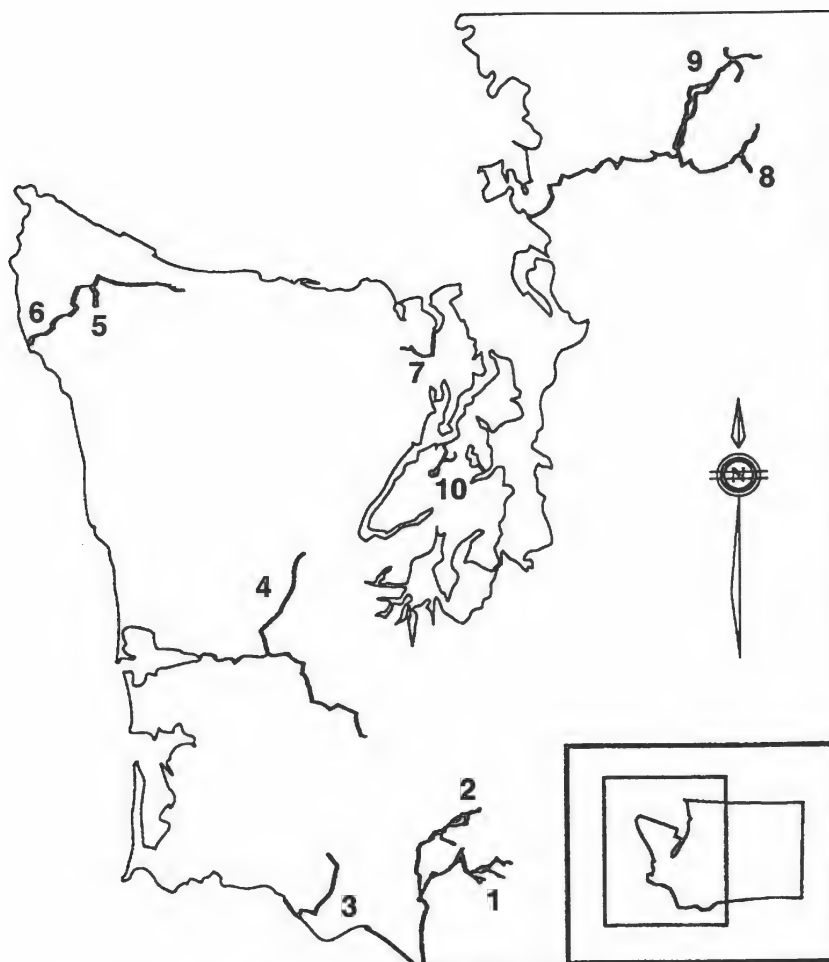


Figure 1. Map of western Washington, indicating sites where gametes were collected for coho salmon incubation studies: (1) Toutle River, (2) Cowlitz River, (3) Elochoman River, (4) Bingham Creek, (5) Bockman Creek, (6) Solduc River, (7) Snow Creek, (8) Clark Creek, (9) Baker River and (10) Big Beef Creek.

TUs to reach 50% hatch than the late run embryos. The early run embryos still required more TUs to 50% hatch than the late run at higher incubation temperatures (9 and 12°), but the TUs to first hatch were similar.

We examined time to hatch at 6°C in more detail, as this is more representative of coho salmon incubation regimes than the higher temperatures. Analysis of data from six populations with at least four families each revealed significant variation (ANOVA, $F = 4.11$, $P < 0.01$) in TUs to hatch

(Table 2). A posteriori analysis (least squares means) revealed that the incubation rate of Cowlitz River coho salmon was slower than that of the other populations, accounting for the most of the variation. There was also variation in TUs to 100% hatch among the three populations with at least 10 families (ANOVA $P < 0.001$, Table 3).

In addition to variation among populations and families, there was also variation within families in hatching time. This was examined in detail in the three populations with the largest numbers of

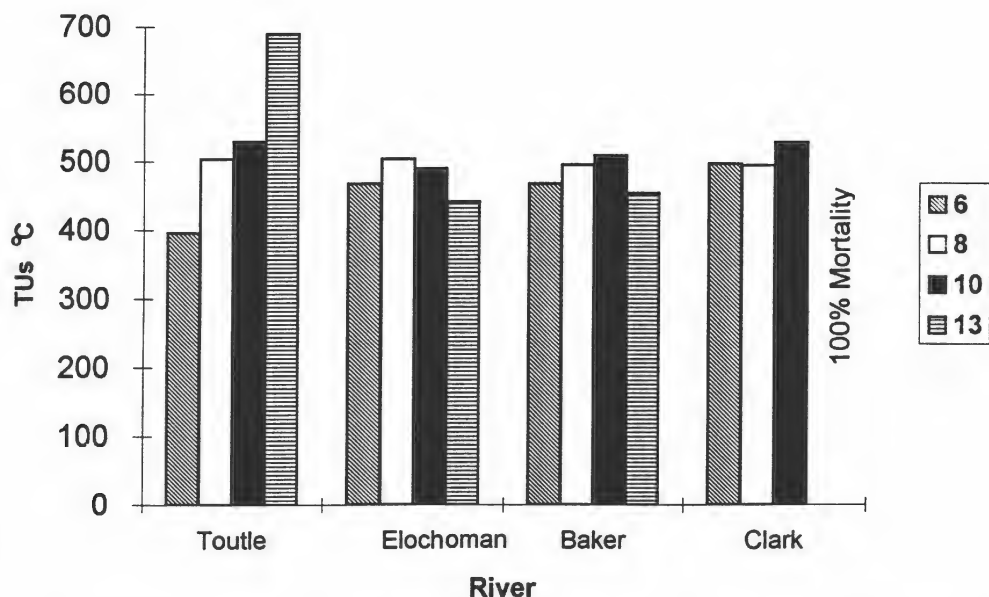


Figure 2. Number of centigrade temperature units (TUs) required for 50% of the embryos from four Washington coho salmon populations to hatch at constant temperatures.

TABLE 1. Average number of temperature units (TUs) to first and 50% hatch in five populations of coho salmon incubated at one of three constant temperatures in 1990. The number of families within each population is designated in parentheses and the range of TUs among families within populations are also indicated.

Population (spawn date)		Incubation Temperature		
		6	9	12
Toutle (6) (1 Nov.)	first:	447 (432-456)	396 (387-405)	432 (420-444)
	50%	471 (450-492)	551 (513-613)	458 (456-468)
Solduc-early (2) (30 Oct.)	first:	513 (510-516)	423 (423)	480 (468-492)
	50%	606 (606)	549 (549)	540 (540)
Solduc-late (5) (27 Nov.)	first:	374 (294-462)	439 (432-450)	478 (456-504)
	50%	471 (456-504)	468 (459-486)	514 (492-540)
Snow (2) (30 Nov.)	first:	423 (420-426)	423 (414-432)	426 (420-432)
	50%	462 (462)	486 (468-504)	482 (477-486)
Cowlitz (4) (5 Dec.)	first:	327 (246-414)	401 (387-423)	414 (408-420)
	50%	438 (420-468)	491 (450-567)	462 (444-480)
Average of populations	first	416.8	416.4	446.0
	50%	489.6	508.2	492.0

families (Big Beef, Bockman and Bingham creeks). Within families, the dates of first and last hatching spanned about 9-14 days (Table 3). Bockman Creek families had the most protracted hatch times and required the most TUs to realize 100% hatch.

We separated families into two groups based on paternal half sibling crosses and evaluated the potential effect male genotype had on TUs to first and 100% hatch (Table 4). The average number of TUs required to first and 100% hatch did not

TABLE 2. Variation among coho salmon populations in TUs to first hatch at 6°C incubation temperature. Data include populations collected in 1990 and 1991.

Population	No. of families	TUs to hatch	Range	SD
Toutle	6	447.0	432-456	8.2
Big Beef	10	429.6	372-450	22.3
Bockman	10	427.8	378-486	32.9
Bingham	13	411.7	360-450	30.3
Solduc-late	5	373.5	294-462	92.0
Cowlitz	4	327.0	246-414	87.3

TABLE 3. Variation in hatching time (difference in TUs and days at 6°C between dates of first and 100% hatching) within families of coho salmon from three Washington populations.

Population	No. of families	Mean range of hatching times	
		TUs (SD)	days (SD)
Bockman Cr.	10	82.2 (24.2)	13.7 (4.0)
Big Beef Cr.	10	52.2 (23.5)	8.7 (3.9)
Bingham Cr.	13	60.9 (33.1)	10.2 (5.5)

differ more than 18 TUs (or 3 days at 6°C), between male genotypes. The widest range in time to first hatch (107 TUs) was observed for the Bockman Creek females crossed with male A; the smallest range was 18 TUs for Big Beef Creek females crossed with male A. When populations were compared, significant differences in TUs to 100% hatch were observed (ANOVA; $P < 0.001$; Tukey multiple comparison).

TABLE 4. Summary of coho salmon half sibling cross results for Washington populations sampled in 1991. The number of females from each population, average egg weights, and average number of thermal units required by broods to first and final hatch are indicated. Each female was crossed with two males (A and B) from their river of origin.

Population (Spawn Date)	# females	egg weight (g)	TUs to 1st hatch		TUs to 100% hatch	
			male A	male B	male A	male B
Bingham (6 Dec.)	7	0.26	405	419	471	474
Big Beef (13 Dec.)	5	0.20	434	425	473	491
Bockman (29 Dec.)	5	0.22	428	427	512	508

Bingham Creek females had the largest eggs (0.26 g; ANOVA, $P = 0.0003$) which began to hatch before either the Big Beef or Bockman Creek broods, and completed hatching at about the same time as the Big Beef broods which had the smallest eggs (average = 0.20 g).

Discussion

Our results confirmed those of studies conducted on British Columbia populations (Beacham and Murray 1990, Murray *et al.* 1990), in that populations, families and individuals all showed variation in temperature-specific incubation rate (i.e., time to hatch). Developmental rate is not equivalent to time to hatch, as environmental conditions such as dissolved oxygen can influence hatching. However, dissolved oxygen levels were at or near saturation during the study, and egg density, substrate, light, and other environmental factors were similar among groups. Therefore, our results probably reflect general patterns of developmental rate in the populations.

Male genotype strongly influences the incubation and developmental rate of pink, chum and sockeye salmon embryos (Withler and Morley 1970, Wood and Foote 1990). However, we did not detect a significant difference in incubation times due to paternal genotype in this study (Table 4). The maternal effect, imparted by egg size (Beacham and Murray 1990), interacts with the male "rate determining" genotype resulting in developmental phenotypes that may be adaptive (Wood and Foote 1990). In this study, Bingham Creek females had significantly larger eggs than either the Big Beef or Bockman Creek broods, but completed hatching in about the same number of

TUs as the Big Beef population which had the smallest eggs.

As with sockeye salmon (Brannon 1987), and other species (Beacham and Murray 1990), coho salmon incubation generally displays a compensatory response to increasing temperatures up to about 10°C. That is, while incubation requires fewer days at higher temperatures, more TUs are required so that development does not proceed as rapidly as would occur if a fixed number of TUs were required. The effect of this compensation is to reduce the variation in emergence date for a given distribution of spawning dates. However, this compensatory relationship was much more pronounced in some populations than others, hence projections of incubation rate based on general models will have some error. Moreover, the compensation is most obvious at temperatures below those in our study (e.g., Tang *et al.* 1987). Little compensation was observed over the range of temperatures that we used and some reverse compensation (i.e., fewer TUs at high temperatures) was observed (e.g., Figure 2), consistent with Tang *et al.* (1987).

A species-specific model of coho salmon incubation, based primarily on British Columbia data (Model 4 of Beacham and Murray 1990), predicted somewhat earlier hatching than we observed. The model estimated 460 TUs to 50% hatch at 6°C compared with the mean of 490 (i.e., 5 days) from five populations (Table 1). The 50% dates were not recorded for the Bingham, Bockman and Big Beef creek populations but interpolated 50% dates were 494, 513 and 516 TUs, respectively. Tang *et al.* (1987) reported 492 TUs to 50% hatch for coho from Washington's Dungeness River, similar to our average. However, the populations that we studied incubated more rapidly than the Skagit River coho salmon reported by Graybill *et al.* (1979), which required 573 TUs to 50% hatch at 6.1°C. Populations from colder regions tend to require fewer TUs to hatch than those from warmer regions (Beacham and Murray 1989, Murray *et al.* 1990). Assuming that British Columbia temperatures are likely to be colder than those in Washington, the tendency for Washington

populations to incubate more slowly than British Columbia populations is not unexpected.

In addition to the variation among populations and families in incubation rate, we also observed variation in hatching date among individuals within families. The first and last individuals to hatch within a family were separated by about 9–14 d. The variation can be magnified at emergence, as Mason (1976) reported variation in emergence from a simulated redd of 20–23 d within full-sibling families. Experiments with Atlantic salmon (*Salmo salar*) indicated that the variation in first feeding date within families leads to differences in social dominance, growth rate and duration of freshwater residence (Metcalf and Thorpe 1992).

Coho salmon populations in the Pacific Northwest often show very protracted spawning periods (Sandercock 1991). Temperature compensation and variation in TUs to emergence between early and late spawners (Brannon 1987) will tend to compress the time of fry emergence. However, the range of spawning dates and variation in development among and within families will generally result in an extended period of emergence. This pattern, combined with variation in fry size related to egg size and family-specific differences in growth and distribution (Quinn *et al.* 1994), may lead to great variation among families in fry size and social status at the end of the summer. Size is also related to overwinter survival in freshwater (Hartman *et al.* 1987), duration of freshwater residence (Holby 1988) and marine survival (Holby *et al.* 1990) in coho salmon. Thus, factors that affect the average incubation rate or the variation among and within families may substantially affect the fitness of young salmon.

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Literature Cited

Beacham, T. D., and C. B. Murray. 1986. Comparative developmental biology of pink salmon, *Oncorhynchus gorbuscha*, in southern British Columbia. J. Fish Biol. 28:233–246.

———. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. 44:244–261.

- _____. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. *Can. J. Zool.* 67:2081-2089.
- _____. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Trans. Amer. Fish. Soc.* 119:927-945.
- Becker, C. D., D. A. Neitzel, and C. S. Abernethy. 1983. Effects of dewatering on chinook salmon redds: tolerance of four developmental phases to one-time dewatering. *N. Amer. J. Fish. Mgmt.* 3: 373-382.
- Brannon, E. L. 1987. Mechanisms stabilizing salmonid fry emergence timing. *Can. Sp. Publ. Fish. Aquat. Sci.* 96:120-124.
- Godin, J.-G. J. 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. In E. L. Brannon and E. O. Salo, (eds.). *Proceedings of the salmon and trout migratory behavior symposium*. School of Fisheries, University of Washington, Seattle, Washington. pp. 22-50.
- Graybill, J. P., R. L. Burgner, J. C. Gislason, P. E. Huffman, K. H. Wyman, R. G. Gibbons, K. W. Kurko, Q. J. Stober, T. W. Fagnan, A. P. Stayman and D. M. Eggers. 1979. Assessment of the reservoir-related effects of the Skagit project on downstream fishery resources of the Skagit River. Final Report for City of Seattle, Department of Lighting, Seattle, Washington. Univ. of Washington, College of Fisheries, Fisheries Research Institute.
- Hartman, G., J. C. Scrivener, L. B. Holtby, and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish populations processes in Carnation Creek, a coastal rain forest stream in British Columbia. In E. O. Salo and T. W. Cundy, (eds.). *Streamside management: forestry and fishery interactions*. Institute of Forest Resources, Univ. of Washington, Seattle. pp. 330-372.
- Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 45:502-515.
- Holtby, L. B. and J. C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) returning to Carnation Creek, British Columbia. *Can. Sp. Publ. Fish. Aquat. Sci.* 105:62-81.
- Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 47:2181-2194.
- Johnson, S. C., G. A. Chapman, and D. G. Stevens. 1989. Relationships between temperature units and sensitivity to handling for coho salmon and rainbow trout embryos. *Prog. Fish-Cult.* 51: 61-68.
- Mason, J. C. 1976. Some features of coho salmon, *Oncorhynchus kisutch*, fry emergence from simulated redds and concurrent changes in photobehavior. *Fish. Bull.* 74:167-175.
- Metcalfe, N. B., and J. E. Thorpe. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* 41(Suppl. B):93-99.
- Murray, C. B., T. D. Beacham, and J. D. McPhail. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (*Oncorhynchus kisutch*) in British Columbia. *Can. J. Zool.* 68:347-358.
- Nehlsen, W., J.E. Williams, and J.A. Lichtowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- Nickelson, T.E., J.W. Nicholas, A.M. McGie, R.B. Lindsay, D.L. Bottom, R.J. Kieser and S.E. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Dept. Fish & Wildlife. 83 p.
- Quinn, T.P., A.H. Dittman, N.P. Peterson and E. Volk. 1994. Spatial distribution, survival and growth of sibling groups of juvenile coho salmon (*Oncorhynchus kisutch*) in an experimental stream channel. *Can. J. Zool.* 72: 2119-2123.
- Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. In R.C. Simon and P.A. Larkin, (eds.), *The stock concept in Pacific salmon*. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver. pp. 19-160.
- Saunderscock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In C. Groot and L. Margolis, (eds.), *Pacific salmon life histories*. University of British Columbia Press, Vancouver. pp. 395-445.
- Sullivan, K. J., J. L. Tooley, G. Doughty, J. E. Caldwell, and P. Knudsen. 1990. Evaluation of prediction models and characterization of stream temperature regimes in Washington. *Timber/Fish/Wildlife Rep. No. TFW-WQ3-90-006*. Olympia, Washington, Wash. Dept. Nat. Resources. 224 p.
- Tang, J., M. D. Bryant, and E. L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. *Prog. Fish-Cult.* 49:167-174.
- Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98:185-207.
- Thedinga, J. F., M. L. Murphy, J. Heifitz, K. V. Koski, and S. W. Johnson. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) in southeast Alaska streams. *Can. J. Fish. Aquat. Sci.* 46:1383-1391.
- Washington Department of Fisheries, Washington Department of Wildlife, and Western Washington Treaty Indian Tribes. 1993. 1992 Washington state salmon and steelhead stock inventory. Olympia, Washington. 212 p.
- Withler, F. C., and R. B. Morley. 1970. Sex-related parental influences on early development of Pacific salmon. *J. Fish. Res. Board Can.* 27:2197-2214.
- Wood, C. C. and C. J. Foote. 1990. Genetic differences in the early development and growth of sympatric sockeye salmon and kokanee (*Oncorhynchus nerka*), and their hybrids. *Can. J. Fish. Aquat. Sci.* 47:2250-2260.

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and

Chad Gubala, ManTech Environmental Technology, Inc., 200 SW 35th St., Corvallis, Oregon 97333

Limnology of Sawtooth Valley Lakes with Respect to Potential Growth of Juvenile Snake River Sockeye Salmon

Abstract

Recovery efforts for Snake River sockeye salmon were initiated in 1991 in response to a decline in the number of returning adults and listing of this population under the Endangered Species Act. We examined limnological conditions in five nursery lakes within the historical range of this population and emphasized factors that likely affect the growth potential of juvenile sockeye salmon. Results of this sampling were intended to facilitate management decisions concerning strategies for restocking progeny from a capture brood-stock program. Temperature, oxygen, light, chlorophyll, phytoplankton, and zooplankton were sampled in each lake from May through October of 1992. Results from limnological sampling indicated that all five lakes would be suitable for rearing juvenile sockeye, but that the lakes varied considerably in the species composition and abundance of zooplankton. Our results indicated that sockeye salmon would not be limited by oxygen or temperature conditions in any of the five lakes. Light levels were suitable for visual feeding to near bottom depths in three of the lakes (Pettit, Stanley, and Yellow Belly) and through 70-90% of the water column in the other two lakes (Redfish and Alturas Lakes). We ranked the five lakes based on growth potential of juvenile sockeye using published relationships of limnological variables and fish growth. Zooplankton food among lakes resulted in pronounced differences in the growth potential of juvenile sockeye salmon suggesting the zooplankton foraging/bioenergetics model was more suited for predictions of sockeye growth in these systems than the other relationships compared. Although growth potential for juvenile sockeye appeared better in three of the lakes, all five lakes are relatively unproductive. Thus a whole-lake fertilization, similar to nutrient enhancement approaches used in Alaskan and British Columbian sockeye nursery lakes, and the impact of piscivory should be considered before final recommendations for recovery plans are evaluated.

Introduction

In 1991 the National Marine Fisheries Service listed the Snake River stock of sockeye salmon (*Oncorhynchus nerka*) as endangered under the Endangered Species Act. Five high-elevation lakes in the Sawtooth Valley of Idaho were formerly habitat for these anadromous fish. After residing in the lakes for 1-2 years, the juvenile sockeye smolted and began their 1400 km migration to the Pacific Ocean via the Salmon, Snake and Columbia Rivers. After 2-3 years in the ocean, mature adults returned to the rearing watersheds to spawn (Bjornn *et al.* 1968; Idaho Fish and Game, pers. comm). Historically, returning adult sockeye salmon likely exceeded 10,000 fish (Evermann 1896, cited in Bjornn *et al.* 1968), and returned to at least five lakes in the Sawtooth Valley. As late as the 1950's numbers exceeding 4,000 were reported (Bjornn *et al.* 1968). Since that time the number of returning adults has declined such that only four individuals returned in 1991 and one

in 1992. The decline of this stock is likely due to a combination of problems associated with passage through dams on the Columbia, Snake and Salmon River systems and commercial and recreational fishing pressure.

In the fall of 1991 we began an assessment of the rearing habitats for juvenile sockeye salmon in five Sawtooth Valley Lakes (Redfish, Alturas, Pettit, Stanley and Yellow Belly Lakes). We examined a variety of limnological conditions that could affect the ability of each of the lakes to support growth and improve survival of juvenile sockeye salmon. Progeny from the four returning adult fish and the out-migrant smolts in 1991 comprise a captive brood-stock for this endangered species unit. One of the goals of our research program was to compare the rearing environments of each of the five lakes to help fisheries managers evaluate strategies for releasing juveniles from the brood-stock program back into the lakes.

Sockeye salmon are cold-water fishes that prefer temperatures less than 15°C and oxygen conditions greater than 5 mg L⁻¹ (Brett 1983; Kyle *et al.* 1988). They are visually feeding zooplanktivores vulnerable to a variety of piscivorous fishes (Burgner 1992). Studies have suggested that

¹To whom correspondence should be addressed.

²Current address: SWCA Inc., Environmental Consultants; 56 W. 400 South, Suite 201, Salt Lake City, UT 84101

growth and survival of juvenile *O. nerka* in lakes are closely linked to zooplankton biomass (Hyatt and Stockner 1985), chlorophyll *a* (Reiman and Meyers 1992), and volume of the euphotic zone (Koenings and Burkett 1987). In this paper we present information on lake morphometry, temperature, oxygen, and light profiles, and phytoplankton and zooplankton populations in the lakes. We focused on seasonal and depth-related differences. We then compared these limnological conditions among the lakes to assess the potential production of juvenile sockeye salmon in each, and used this comparison to evaluate management strategies designed to assist in the recovery of this population.

Methods

The routine sampling reported here of the five lakes began in May of 1992 and ended in October of 1992. Lakes were sampled 3-4 times in May and June and once every 10 days for the rest of the season. Additional temperature and oxygen profiles were measured in some of the lakes in April and November.

At the deep station in each lake, we sampled temperature, oxygen, and light profiles, chlorophyll concentrations, and phytoplankton and zooplankton populations. Chlorophyll and zooplankton samples were collected at two additional stations on each lake. The methodology used is described in greater detail below for each variable measured.

Lake Morphometry

We used an echo-sounder linked with a global positioning system (GPS) to chart the bathymetry of each lake in October 1992 using the methodology of Gubala *et al.* (1994). Depth data from an American Pioneer Fishscope II echo-sounder (6.5° beam angle, 160 kHz), and position data from a Trimble Pathfinder Professional GPS unit were recorded on a data logger at 2-second intervals as our boat cruised at 2-4 m/s along transects in each lake. For the different sized lakes we recorded between 860 and 1540 depth and position points. Because the U.S. Department of Defense degrades the satellite-transmitted GPS data through Selective Availability, uncorrected location measurements can be up to 100-m in error. Consequently, we corrected our position data by recording deviations of a GPS unit fixed at the Sawtooth National Fish Hatchery which is within 24-km from the furthest lake. The GPS positions recorded in the boat were then differentially corrected for these devia-

tions with Asset Survey software of Tribble Navigation, Ltd. giving a final accuracy of approximately ± 2 -m. In addition to the GPS locations, we added 160-570 points for the perimeters of the lakes by digitizing USGS topographic maps (7.5' series). Because we did our survey in October at the end of the hydrologic year during a six-year drought, we increased each of our depth readings by 0.5-m to more closely represent normal water conditions in the lakes.

Temperature and Oxygen

Vertical profiles of temperature and oxygen were taken at 1-5-m intervals with a YSI Model 58 Dissolved Oxygen Meter. Periodically throughout the field season, the oxygen content of water from three depths was measured with the Winkler method to verify the accuracy of the YSI probe (APHA 1992).

Light Extinction

Vertical profiles of light intensity were measured at the deep station using a submersible Li-Cor Model LI-188B photometer. Measurements were taken at 2-m increments from the surface to 28-m deep. The extinction coefficient (Wetzel 1983) was then calculated as the slope of the regression of $\ln$ (% surface intensity) against depth.

Water transparency was also measured at the deep station with a 20-cm black and white Secchi disk and recorded as the mean of the depth where the Secchi disk disappeared and reappeared.

Chemical Analysis of Nutrients

An integrated epilimnetic lake water sample was collected at the deep station in each lake by lowering a weighted 0.64-cm diameter Tygon® tube 6-m into the water column and emptying the contents into a 1-l bottle for chlorophyll *a*, phytoplankton and chemical analysis. Samples for dissolved inorganic nutrient analyses [nitrate-nitrogen (NO_3) and soluble reactive phosphorous (SRP)] were filtered through a 0.45- μm membrane filter 2-6 hours after collection and frozen until analysis. Unfiltered samples were analyzed for total phosphorus (TP) and total Kjeldahl nitrogen (TN).

Chlorophyll and Phytoplankton

In addition to the epilimnetic integrated tube samples described above, on some dates we also

collected metalimnetic and hypolimnetic samples with a Kemmerer water bottle for chlorophyll and taxonomic analyses. For routine analyses of chlorophyll we filtered 50-ml aliquots on 0.45- μ m cellulose acetate membrane filters. On two dates we also fractionated the water sample by filtering with 0.1- μ m and 1.0- μ m Nucleopore membrane filters and 30- μ m Nitex nylon screens to establish the relative chlorophyll content of different size fractions of phytoplankton. The filters were either temporarily frozen or placed directly into 6 ml of 100% buffered methanol and extracted in the dark for 24-48 hr at room temperature. The extracts were then analyzed fluorometrically (Holm-Hansen and Rieman 1978) with a Turner model 111 fluorometer calibrated with standard chlorophyll *a* (Sigma). After the initial reading the samples were acidified with two drops of 1.0 N HCl, and reread to correct for phaeophytin.

We collected samples for algal enumeration and biomass estimates from the same 0-6-m tube samples taken for chlorophyll analyses. Additional samples were occasionally taken in the metalimnion and hypolimnion to examine the change in species composition with depth. We preserved the samples using Lugol's solution and subsequently filtered a single 100 ml aliquot from each depth strata sampled on 0.45- μ m cellulose acetate membrane filters at low vacuum pressures (0.3 atm.). The filters were then cleared and mounted in methacrylic resin following the procedure of Crumpton (1987). Cells were identified and counted at 400X-magnification in 50-100 fields that transversed the filter to take into account the tendency of cells to concentrate on the edge of the filters (Holmes 1962). The dimensions of a minimum of 10 individuals in each taxa were taken, and biovolumes subsequently calculated assuming the algae conformed to fixed geometric shapes.

Zooplankton

Six vertical zooplankton tows were collected on each date using a Wisconsin style zooplankton net measuring 35-cm in diameter and 80-cm long with 80- μ m mesh. A General Oceanics flow meter was used to determine net efficiency and volume sampled. The flow meter was modified on request to General Oceanics to prevent reverse flow of the meter. Zooplankton were sampled over 2 depth ranges, a 10-m to surface tow and a bottom to surface tow, at each of the three stations. Zooplank-

ton were preserved in 10% neutralized formalin solution.

We identified four cladocera (*Daphnia rosea*, *Bosmina longirostris*, *Holopedium gibberum*, *Polphemus pediculus*), one calanoid copepod (*Epischura nevadensis*) and several species of cyclopoid copepods (Thorp and Covich 1991). Zooplankton were enumerated and measured in replicated 1-5 mL sub samples taken with a Hensen-Stempel pipette and placed in a circular counting dish. Individual lengths of each species were measured from each sample and mean length for each taxa was calculated. Biomass was determined for each species using the procedures and linear regression equations described by McCauley (1984) and Koenigs *et al.* (1987).

In addition to our routine zooplankton sampling, mid-summer vertical distribution and diel migration of zooplankton was examined in Redfish and Stanley Lakes by collecting depth-stratified zooplankton tows during day and night periods. Zooplankton were collected using a closing net equipped with a flow meter. Samples were collected from Redfish Lake between 1100-1230 h on 3 August 1992 and between 0-120 h on 4 August 1992. Two replicate samples were collected from each 5-m depth strata from 0-20 m, each 10-m strata from 20-40 m, and each 20-m strata from 40-80 m. Two samples were collected from the bottom-80-m. Samples were collected from Stanley Lake between 1450-1530 h on 2 August and between 100 h-200 h on 3 August. Two replicate samples were collected from each 5-m depth strata from the bottom to the surface. Density of each crustacean taxa were estimated according to the methods cited above. We used an Anova to compare differences in depth distribution of individual zooplankton species by day and night (time-by-depth interaction).

Results

Lake Morphometry

Morphometric characteristics of the five lakes are described in Table 1. The morphometry map of Redfish Lake is shown in Figure 1, and maps of the other four lakes are available in Spaulding (1993). Redfish Lake had the greatest volume, surface area and mean maximum depth. Yellow Belly and Stanley were the smallest lakes in the basin, containing only 4% of the volume of Redfish Lake.

TABLE 1. Morphological characteristics of the five study lakes.

Lake	Area (km ²)	Volume (m ³ × 10 ⁶)	Depth Maximum (m)	Depth Mean (m)
Redfish	6.15	269.9	91	44
Alturas	3.38	108.2	53	32
Pettit	1.62	45.0	52	28
Yellow Belly	0.73	10.3	26	14
Stanley	0.81	10.4	26	13

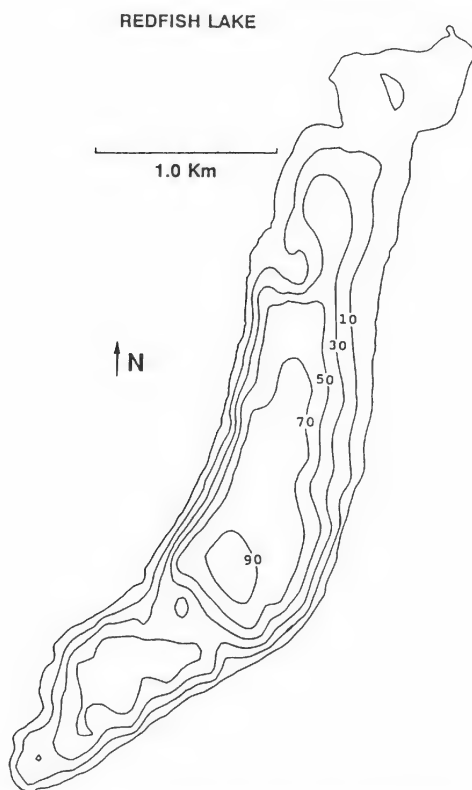


Figure 1. Morphometric map with depth contours in meters for Redfish Lake.

Temperature and Oxygen

Seasonal development of thermal stratification was similar in each of the lakes. Temperature and oxygen profiles for all five lakes on 31 July 1992 are shown in Figure 2. Maximum surface temperatures reached 18°C, while hypolimnetic temperatures

were 4°C over the eight months sampled. Surface temperatures reached a high of 18°C only for a short period in late July and early August and remained between 12-16°C for the majority of the summer. The thermocline developed in mid-May and was generally located between 8-m and 18-m in the deeper lakes (Redfish, Alturas, and Pettit) and between 8-m and 15-m in the shallower lakes (Stanley and Yellow Belly).

Dissolved oxygen levels in mid-May ranged from 10 mg/L near the surface to 4 mg/L near the bottom of all lakes. The YSI meter readings varied within 0-16% of the Winkler measurements when comparing both different depths and lakes. As thermal stratification evolved, oxygen concentrations were reduced in the hypolimnion of all the lakes. Low levels of dissolved O₂ (< 3 mg/L) were measured at depth in all lakes except Redfish. The low oxygen levels were located a few meters off the bottom in Alturas (45-50 m), Stanley (22-25 m), and Yellow Belly (21-25 m) but were found as shallow as 40-m in Pettit Lake. Pettit, Stanley and Yellow Belly Lakes exhibited prolonged periods where the bottom water remained below 2 mg O₂ / L.

A metalimnetic oxygen maxima of approximately 10 mg/L developed in Alturas, Yellow Belly, Pettit and Stanley lakes in mid-summer. This maxima lasted for as short as 12 days (Pettit) and as long as 2 months (Alturas). Redfish Lake did not develop a distinct metalimnetic oxygen maxima.

Light Extinction and Transparency

The depth of the nominal photic zone (1% light extinction levels) in each lake was approximately 1.5-2 times the Secchi depth. The relationship between the 1% light level and the Secchi depth was linear when data for all five lakes was combined ($y = 4.5 + 1.5x$; $R^2 = 0.451$). The relationship was much tighter if light extinction and Secchi were examined for each lake individually.

The Sawtooth lakes were quite clear, with Secchi depth transparencies ranging from 5-18 m (Figure 3). In most of the lakes transparencies increased, from May through September. Transparencies in Stanley Lake were lower than in the other lakes and had a different seasonal pattern. Much of the week-week variability in Secchi depths was due to calm versus wavy conditions that affected our measurements.

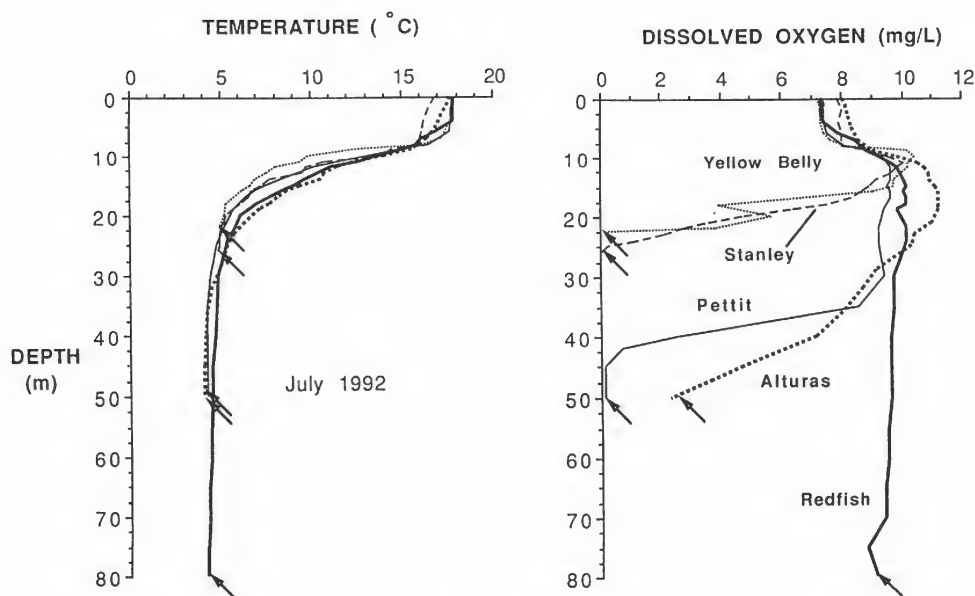


Figure 2. Temperature and oxygen profiles for each lake measured on 31 July 1992 at the deep station in each lake. The arrows point to the approximate bottom depth of each lake, Redfish Lake max depth = 91 m, Alturas Lake max depth = 53 m, Pettit Lake max depth = 52 m, Yellow Belly Lake max depth = 26 m, and Stanley Lake max depth = 26 m.

Chemical Analysis of Nutrients

Mean seasonal epilimnetic TP and TN concentrations ranged from 6-11- $\mu\text{g/L}$ and 66-102- $\mu\text{g/L}$ respectively, and TN:TP ratios ranged from a low of 6:1 to a high of 11.5:1. Mean seasonal concentrations of dissolved nutrients were low with SRP and NO_3 ranging from undetectable values to 2.3 $\mu\text{g/L}$ and 4.0-9.4 $\mu\text{g/L}$ respectively. Inter-year and seasonal fluctuations or climate and limnological conditions have a large effect on Sawtooth Valley Lakes nutrient composition, but these fluctuations do not effect the relative rankings of productivity among the lakes.

Chlorophyll and Phytoplankton

Mean epilimnetic concentration of chlorophyll *a* for the five lakes ranged from 0.44 to 0.90 mg/m^3 , with individual values ranging from 0.22-2.38 mg/m^3 . The highest epilimnetic chlorophyll concentration for each lake occurred on 9 May, when the first measurements were taken (Figure 4) approximately 2 weeks after spring overturn. The minimum epilimnetic chlorophyll concentration for

each lake occurred in July and August. Epilimnetic chlorophyll increased during autumn as the thermocline began to erode.

Depth profiles indicated pronounced increases of chlorophyll *a* in the metalimnia and hypolimnia of the lakes. For example, in mid-September in Redfish Lake, epilimnetic chlorophyll *a* concentrations were 0.49 mg/L , but at 40-m they reached 2.27 mg . In most of these lakes the deep chlorophyll maxima were located near the 1% light level where temperatures were 5-6°C (Figure 5). The deep chlorophyll maxima were located approximately 5-10-m below the metalimnetic oxygen maxima.

Size-fractionation of epilimnetic water revealed a similar size distribution of phytoplankton in each of the five lakes (Figure 6a). Seventy-two to 91% of the chlorophyll in the five lakes was distributed in size classes that would be available to herbivorous crustacean zooplankton (0.45-30 μm ; Reynolds 1984). Only 4 to 12% of the phytoplankton in the five lakes was larger than 30 μm . In Redfish Lake, size-fractionation analysis of samples collected at four depths (0-6 m, 15 m, 35 m, and

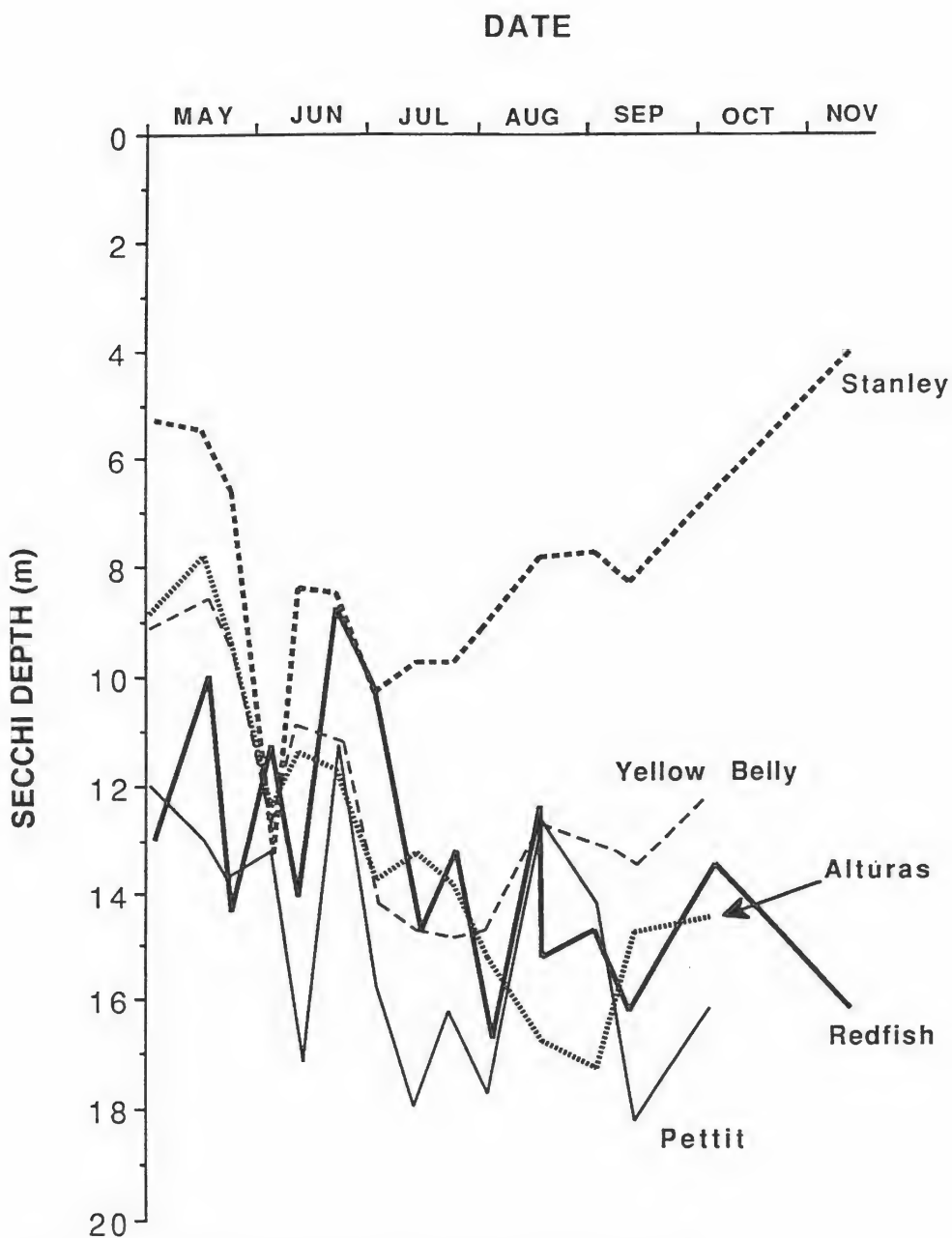


Figure 3. Seasonal distribution of secchi depths measured at the deep station in each lake.

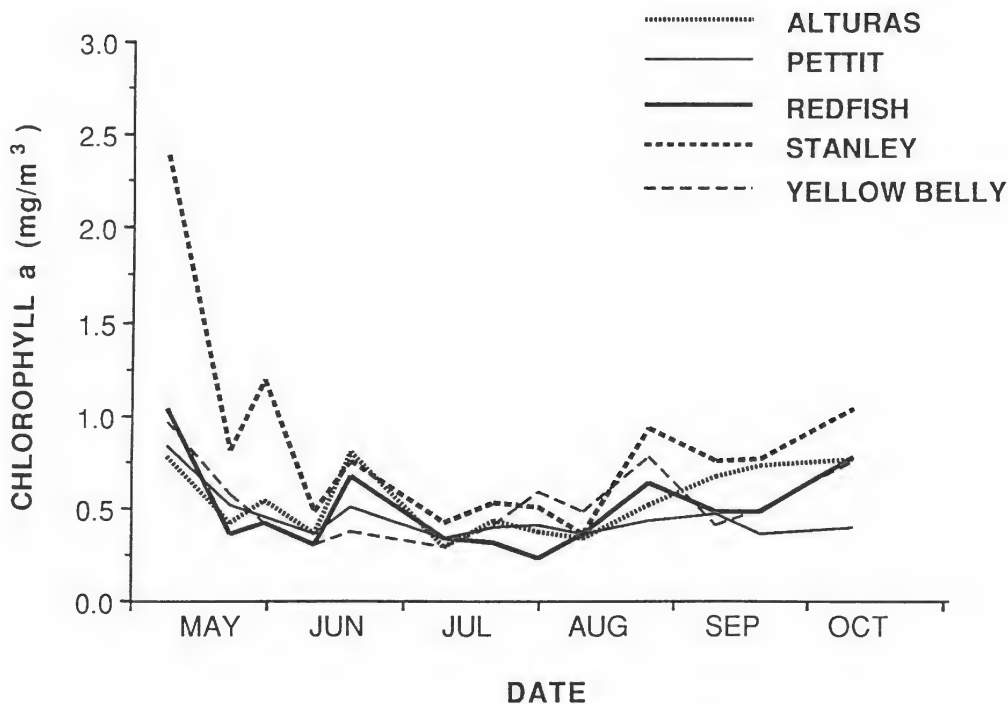


Figure 4. Seasonal distribution of chlorophyll *a* concentrations in the 6-0-m depth strata for all five lakes.

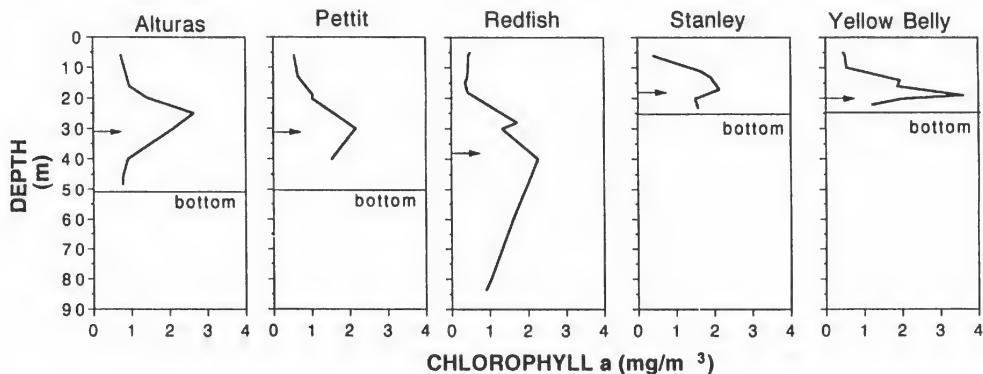


Figure 5. Chlorophyll *a* depth profiles for each lake. The arrows point to the depths of the 1% light extinction depth, and the bottom is shown for the shallower lakes.

80 m) indicated that 60 to 82% of the phytoplankton at each depth was of a grazable size (Figure 6b).

The phytoplankton taxa, exemplified by those in Redfish Lake, were dominated by diatoms (*Cy-*

otella sp., *Tabellaria* sp., and *Fragilaria* sp.), chrysophytes (*Dinobryon* sp.), chlorophytes (*Chlamydomonas* sp. and small chlorococcales), and a small coccoid cyanobacteria. Nearly all of the phytoplankton were small, and the mean

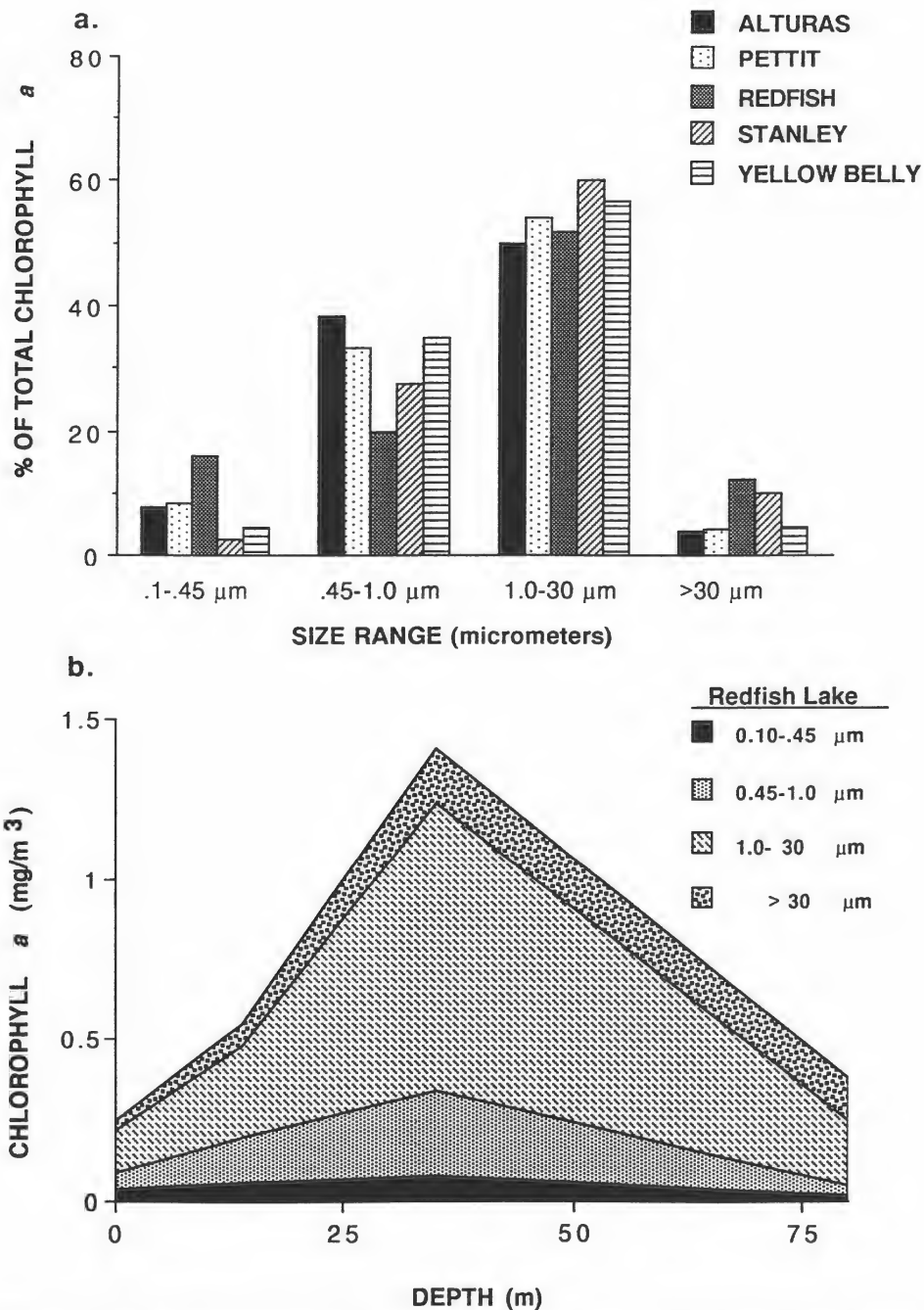


Figure 6. a) Size fractionation of chlorophyll *a* in the epilimnion of all five lakes on 9-11 July 1992. b) Depth-stratified phytoplankton size fractionation for Redfish Lake, 9 July, 1992. Epilimnetic samples were taken with a 0-6 m tube sampler; other discrete samples were collected at 14, 35, and 80-m.

equivalent spherical diameters for all of the taxa ranged from about 4 to 12 μm . Picoplankton ($<1\ \mu\text{m}$) were present and sometimes abundant; however, these microbes were not identified because we were most interested in the primary producers directly available to the macrozooplankton prey of *O. nerka*.

In the epilimnion of Redfish Lake, algal biomass was moderately high from April to May, with a peak in the last two weeks of June (Figure 7a). During spring the community was dominated by *Dinobryon* sp., very small unidentified spherical green algae of the order chlorococcales, and diatoms (principally *Cyclotella* sp., *Tabellaria* sp., and *Fragilaria* sp.). In early July the algal biovolume plunged by an order of magnitude from the spring maximum high, and became dominated by small cyanobacteria and *Dinobryon* until the end of August when diatoms and the green algae *Chlamydomonas* sp. appeared (Figure 7b).

Algal biovolume was lowest in Redfish Lake, and highest in Yellow Belly Lake (Figure 7a). Seasonal changes in algal biovolume in all lakes were variable, but generally indicated higher algal abundance in spring and lower biovolume by mid-summer (Figure 7a). Phytoplankton in the deeper waters of Redfish Lake were more abundant and had a different taxonomic composition than those in the epilimnion. In July, the epilimnetic biovolume was dominated by cyanobacteria (78%), *Dinobryon* sp. (10%), and diatoms (8%). At the top of the metalimnion (14 m), algal biovolume increased slightly due to an increase in *Dinobryon* sp. In the hypolimnion (80 m), the total biovolume was nearly nine times greater than in the epilimnion and was dominated by diatoms. In August, the epilimnion community was composed of diatoms (38% by volume), *Chlamydomonas* sp. (48%) and small chlorococcales (11%). *Chlamydomonas* sp. disappeared in the upper metalimnion (14 m), as diatoms increased to represent 89% of the community. Near the deep chlorophyll maxima (35-m) (Figure 6b), the biovolume was nearly eight times higher than in the epilimnion, and the relatively large or colonial diatoms, *Asterionella* sp., *Synedra* sp., and *Cyclotella* sp. represented 99% of the biovolume (Figure 6b).

Zooplankton

Seasonal patterns of crustacean zooplankton density and biomasses indicated that the epilimnion

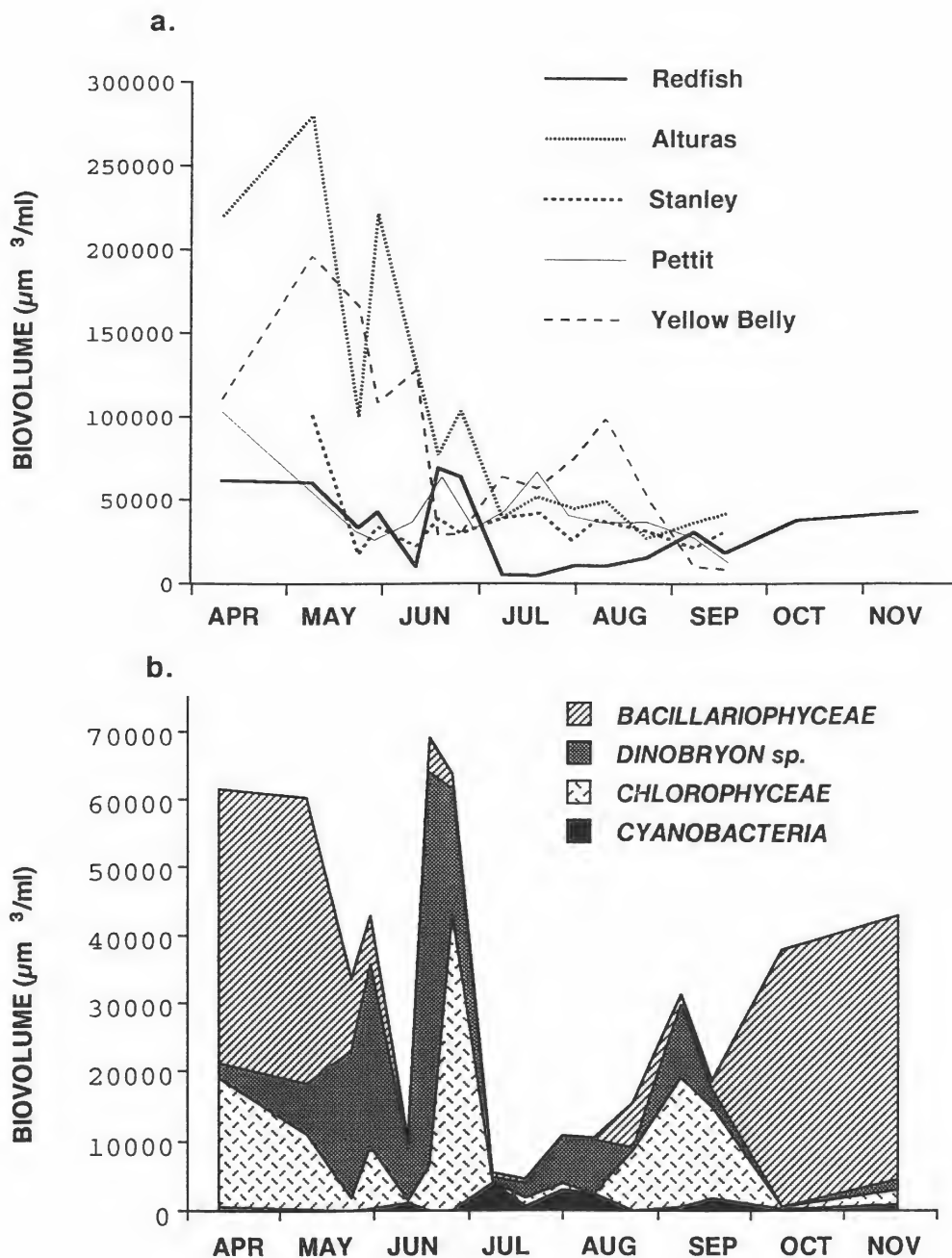
of Redfish and Alturas Lakes contained the lowest biomass throughout the season compared to the other lakes (Figure 8). Pettit Lake had a high density but low biomass of crustaceans early in the season owing to the dominance of small-bodied *Bosmina*. The dominance of *Bosmina* in Alturas Lake throughout the season resulted in moderately high densities of total crustacean zooplankton but consistently low biomass when compared to the other lakes. All five lakes appeared more similar in zooplankton abundance when only density was considered, but total biomass estimates indicated differences among the lakes (Figure 8 a,b).

Redfish and Alturas Lakes had very low biomasses of crustacean zooplankton with *Holopedium* dominating most of the season in Redfish and *Bosmina* dominating in Alturas (Figure 9 a,b). Total crustacean zooplankton biomass remained below 25 $\mu\text{g/l}$ in these lakes in mid-summer. The carnivorous cladoceran *Polyphemus* exhibited a substantial increase in Alturas immediately after the mid-summer decline of *Bosmina* and *Holopedium*. Neither of these two lakes had abundant populations of *Daphnia* or copepods in the epilimnion.

Pettit, Stanley, and Yellow Belly lakes had higher cladoceran densities than Alturas or Redfish (Figure 9 c,d,e). Pettit and Stanley Lakes exhibited a distinct seasonal succession of cladoceran species in which *Holopedium* comprised most of the biomass in early summer, and *Daphnia* dominated during late summer and early fall. The predatory copepod *Epischura* contributed to the crustacean biomass of Stanley Lake, and *Daphnia* dominated the zooplankton of Yellow Belly throughout the year.

Zooplankton densities estimated from bottom to surface tows were generally lower than values estimated in the epilimnion in all lakes. Cyclopoid copepods, however, were much more abundant in the hypolimnion in each of the lakes. *Holopedium* and *Epischura* were more abundant in the epilimnion than in the hypolimnion. Densities of *Bosmina* and *Daphnia* were similar in epilimnetic and whole water column tows. Whole water column tows may have over-emphasized zooplankton taxa that occurred in the hypolimnion because of the decrease in net efficiency as the net was pulled through the deep chlorophyll maxima that contained net-clogging filamentous algae (Figure 6 b).

Vertical distribution of zooplankton in Redfish Lake on 3 August 1992 indicated that different zooplankton taxa segregated according to depth



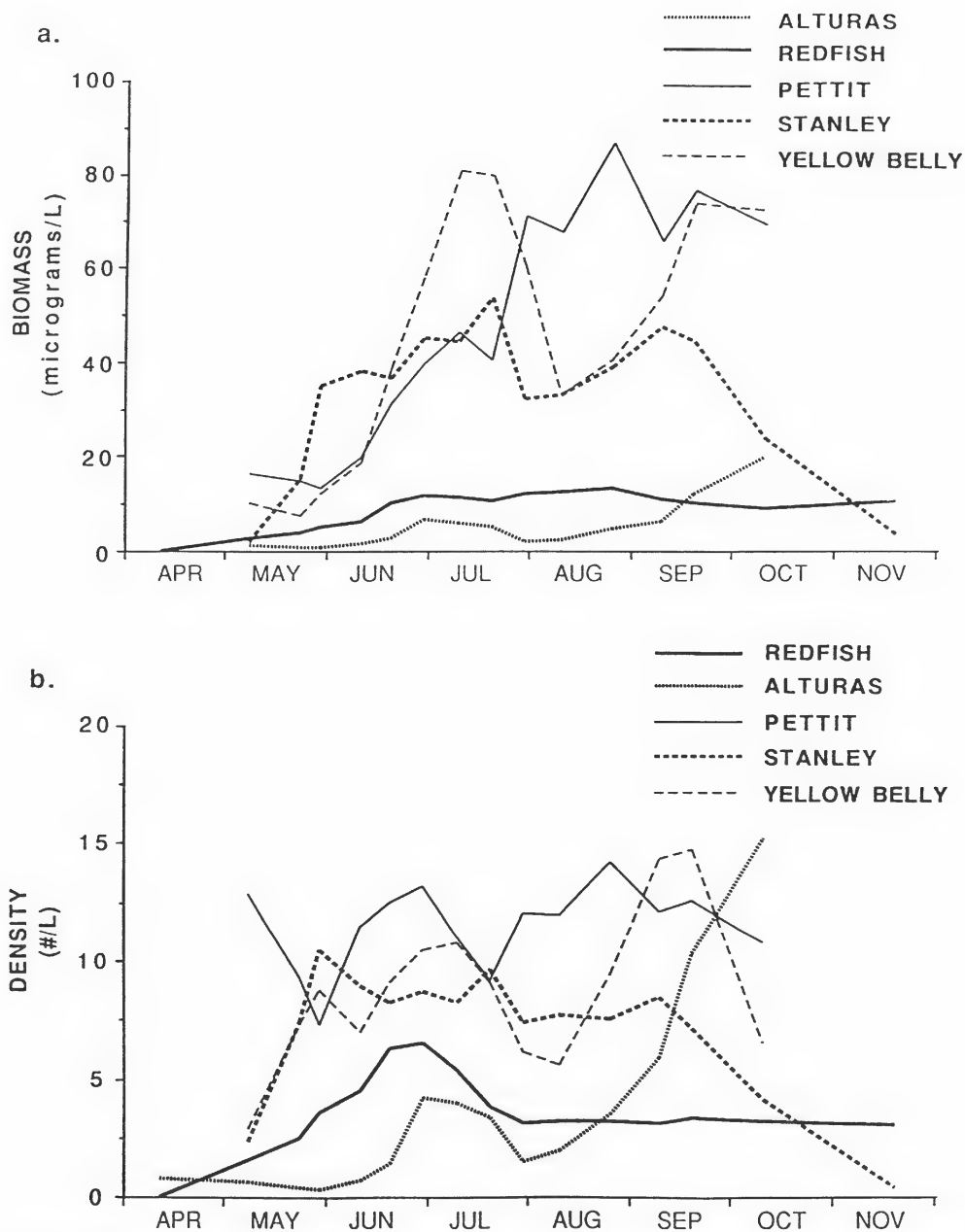


Figure 8. Seasonal distribution of total crustacean zooplankton in epilimnetic tows in the five lakes: a) biomass b) density. Data were smoothed with a 3-point running mean.

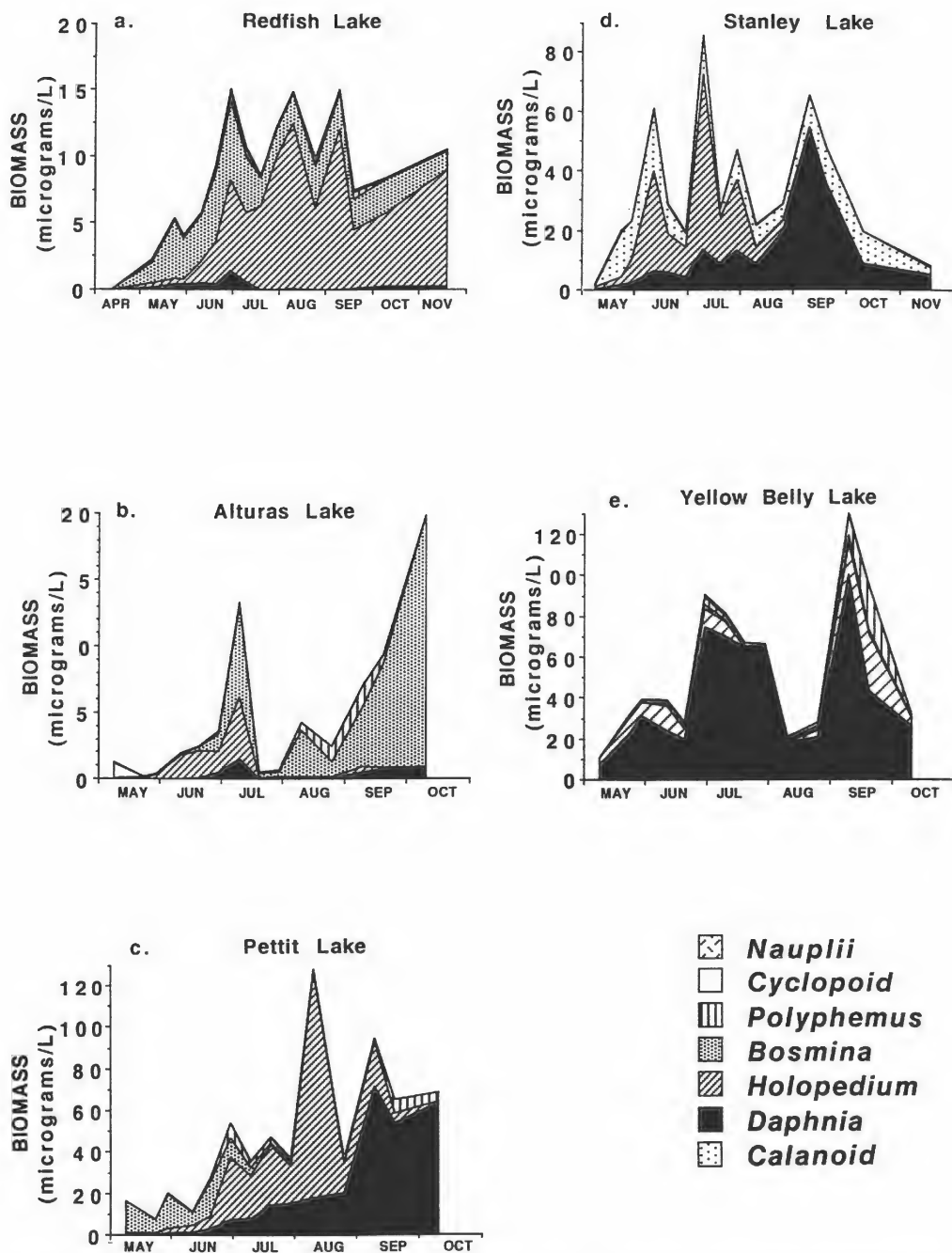


Figure 9. (a-e). Seasonal distribution of zooplankton species biomass composition in the epilimnion of all five lakes. Note the different y-axes scales used: (0-20 $\mu\text{g/l}$) on the Redfish and Alturas Lakes, (0-120 $\mu\text{g/l}$) on the Pettit, and Yellow Belly Lakes graphs, and (0-90 $\mu\text{g/l}$) on the Stanley Lake graph.

during the day (Figure 10). At mid-day, *Holopedium* was concentrated in the epilimnion and metalimnion attaining peak densities of 4 individuals L^{-1} in the 5-10-m strata. Cyclopoid copepods were most abundant in the hypolimnion attaining peak densities of 1.7 individuals L^{-1} in the bottom strata. *Bosmina* was present throughout the water column but was more concentrated in the deeper waters. *Daphnia* and *Polypheumus* were present in very low numbers throughout the water column.

An ANOVA examining the time-by-depth interaction suggested that the common crustaceans moved up in the water column during the night. *Holopedium* moved slightly from a mean depth of 10-m during the day to 7-m at night ($F_{1/8}=17.8$, $P<0.001$). *Bosmina* migrated extensively from a mean depth of 46-m during the day to 15-m at night ($F_{1/8}=28.8$, $P<0.001$). Cyclopoid copepods exhibited small movements, migrating from a mean depth of 71-m during the day to 58-m at night, but this difference was not significant ($F_{1/8}=0.38$, $P>0.05$).

The vertical distribution of crustacean zooplankton in Stanley Lake was similar to that of Redfish. During the day *Holopedium* was concentrated in the epilimnion, whereas cyclopoid copepods were concentrated in the hypolimnion. *Daphnia* was present throughout the water column but most abundant in the 10-15-m strata. *Epischura* was most abundant in the upper portion of the water column. An ANOVA indicated that diel differences in vertical distribution were significant for *Daphnia* which occupied a mean depth of 11.8-m during the day and 7.9-m during the night than during the day ($F_{1/4}=4.70$, $P<0.05$). *Holopedium* also was located higher in the water column during the night ($F_{1/4}=8.46$, $P<0.05$). Cyclopoid copepods became more concentrated near the bottom of the lake during the night ($F_{1/4}=21.5$, $P<0.01$). No significant differences in diel changes in the vertical distribution of *Epischura* was apparent in Stanley Lake.

Discussion

Results from the limnological sampling indicated that all five lakes are suitable for rearing juvenile sockeye salmon. Temperature and oxygen conditions within a large portion of each lake fell within the tolerance range of sockeye ($<17^{\circ}C$, >5 mg O_2/L , LeBrasseur *et al.* 1978). In Redfish Lake

nearly all of the water column was within these tolerance ranges throughout the season. In the other lakes the bottom 5-15-m of water contained insufficient oxygen to support permanent occupation by sockeye salmon. Subsequent sampling in these lakes has indicated that the low deep hypolimnetic oxygen levels are due to incomplete mixing of the water column in the spring and/or fall (Luecke and Wurstbaugh, unpublished data).

The ample volume of water with suitable temperature and oxygen conditions suggests that sockeye salmon could behaviorally select water depths that provide best conditions for growth and survival. Brett *et al.* (1969) suggest that sockeye should choose water temperatures around $15^{\circ}C$ to optimize conversion efficiency of food. This hypothesis would predict that juvenile sockeye salmon would reside in epilimnetic waters in the five lakes. Brett (1971) subsequently showed, however, that salmon seldom use temperatures of $15^{\circ}C$.

Light conditions indicated that sockeye salmon could feed visually during the day near the bottom of Stanley, Pettit and Yellow Belly Lakes (0.1% of surface light, Ali 1959, Levy 1990). Conversely, fish would cross the 0.1% surface light isolume at approximately 45-m in Alturas and 55-m in Redfish Lake. Although zooplankton densities are low in all the lakes, the high light environment should facilitate foraging juvenile sockeye salmon.

Levy (1990) indicated that juvenile sockeye salmon in lakes with piscivorous fish populations were concentrated during the day at depths (and light levels) that could be predicted from light extinction (k) according to the relationship:

$$\text{Depth (m)} = 15.4 k^{-1} + 1.23$$

These results caused Levy (1990) to hypothesize that juvenile sockeye salmon should behave so as to avoid visual predators during the day and choose an energetically efficient temperature at night. His hypothesis predicts that juvenile sockeye salmon would reside at the bottom of all five lakes during the day, and move to epilimnetic areas at night. The high light environment in the Sawtooth Valley Lakes may make juvenile sockeye salmon particularly vulnerable to fish piscivores in that little daytime refuge exists for these prey fish.

The nutrient and chlorophyll data suggest that all of the Sawtooth Valley lakes are oligotrophic, and that fish production will consequently be

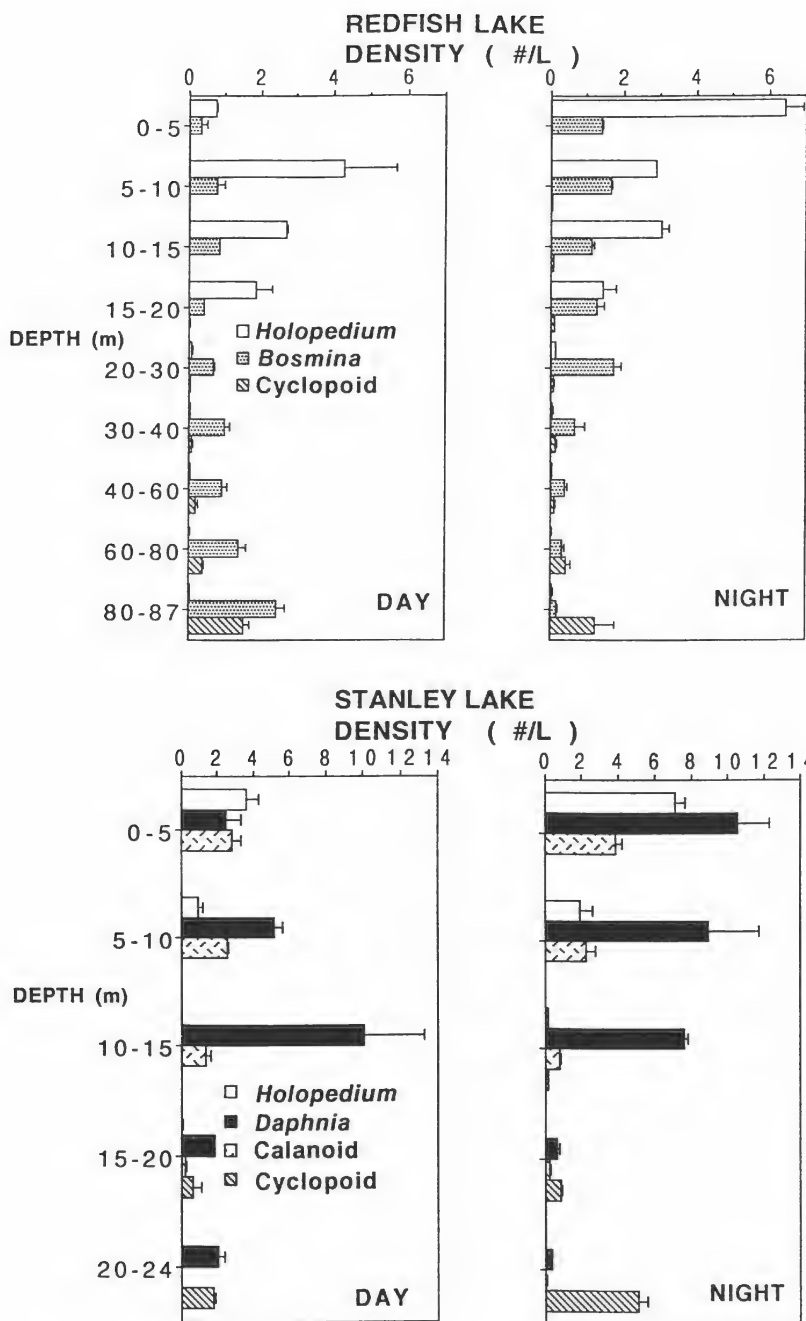


Figure 10. Diel vertical distribution of zooplankton densities from Redfish Lake (above) and Stanley Lake (below), 3-4 August 1992. Error bars denote the one-half range of two samples.

TABLE 2. Potential growth or production of juvenile sockeye salmon in five lakes of the Sawtooth Valley. Chl (chlorophyll) and Secchi relationships are from Rieman and Meyers (1992), the EZ (euphotic zone) model from Koenings and Burkett (1987), and the ZOOP (zooplankton/energetics) model is from Budy *et al.* (1994). Values represent predictions of the model in either lengths of age-0 fish in September (mm TL) or production of smolts (# / ha). The number in parentheses refers to the rank given each lake in terms of sockeye production for a particular model. The last row of data refers to *O. nerka* collected in mid-water trawls. NA indicates that no data were collected.

Model	Lake				
	Redfish	Alturas	Pettit	Stanley	Yellow B.
Chl (mm TL)	99	100	98	108	99
(Rank)	(3.5)	(2)	(5)	(1)	(3.5)
Secchi (mm TL)	65	67	43	134	79
(Rank)	(4)	(3)	(5)	(1)	(2)
EZ (smolts/ha)	791	547	780	425	386
(Rank)	(1)	(3)	(2)	(4)	(5)
Zoop (mm TL)	63	50	105	105	112
(Rank)	(4)	(5)	(3)	(2)	(1)
Actual (mm TL)	65	55	NA	95	NA
(Rank)	(2)	(3)		(1)	

limited by basic lake productivity. Although we did not measure primary production directly in this study, subsequent work in Redfish Lake has shown a close correlation between epilimnetic chlorophyll concentrations and primary production (Gross *et al.* 1994), as it often is in oligotrophic lakes (i.e. Stockner and Hyatt 1984). Furthermore, both nutrient and chlorophyll concentrations have been used successfully to predict fish production in lentic systems (Carline 1986). The presence of deep-chlorophyll layers in the lakes may, however, confound predictions based on epilimnetic chlorophyll levels, as a considerable amount of primary production in these lakes may occur in the metalimnia and hypolimnia (Shortreed and Stockner 1990).

A number of authors have derived sockeye growth or production values from nursery lakes given limnological information of the type collected in our study. Rieman and Meyers (1992) indicted that Secchi transparency and epilimnetic chlorophyll levels provided the best predictors of the growth of *O. nerka* in Idaho Lakes. Koenings and Burkett (1987) described a significant positive relationship between the volume of the euphotic zone and the density of sockeye smolts in a series of Alaskan lakes. In addition to these regression approaches, Walters *et al.* (1991) and Budy *et al.* (1993) have constructed simulation models to examine the relationship between zooplankton biomass and juvenile sockeye growth within a bioenergetics context (Beauchamp *et al.* 1989).

These approaches can be used to assess the potential for each of the five lakes to serve as a rearing environment for the endangered stock of sockeye salmon. These models provide a different ranking of the lakes in terms of sockeye growth potential (Table 2). The chlorophyll and Secchi relationships (Rieman and Myers 1992) indicated that Stanley would provide the best conditions for juvenile growth and that Pettit would provide the worst. The euphotic zone model (Koenings and Burkett 1987) predicted that Redfish and Pettit would produce almost 800 smolts per hectare (Table 2), whereas Stanley and Yellow Belly would produce only half that amount. Preliminary simulations of a zooplankton foraging-energetics model (Budy *et al.* 1993) suggest that growth of juvenile sockeye salmon would be greatest in Yellow Belly, Stanley, and Pettit Lakes (descending order) and poorest in Redfish and Alturas (Table 2).

A comparison of the weight of *O. nerka* captured in mid-water trawls in September of 1992 with the rankings of each of the potential sockeye growth or production models suggests that the Secchi and zooplankton models provided the closest fit to the observed growth of juvenile *O. nerka* in the lakes (Table 2). The chlorophyll model predicted larger fish than occurred in trawl catches from the lakes. Predictions from the Secchi model were similar to the observed size of fish captured in Redfish Lake, but predicted larger fish than were captured in Stanley Lake. The zooplankton

simulation model correctly ranked the growth of fish in the lakes, but the range of fish lengths among the lakes was greater than predictions from the simulations. It was unlikely that the euphotic zone production model would provide a good ranking of potential production of sockeye in these highly transparent lakes in that this model was designed for use with stained or glacial lakes where light limitation of phytoplankton is common.

Results of this study indicated that each of the five lakes could support juvenile sockeye salmon, but that the potential growth and therefore survival (Peterson and DeAngelis 1993) of these fishes would vary several-fold among the lakes. Further, based on limnological information presented here, the lakes can all be considered oligotrophic and thus relatively unproductive rearing lakes for sockeye salmon. The higher zooplankton biomasses in Stanley, Pettit and Yellow Belly Lakes indicates that growth of juvenile sockeye salmon would be greater in these lakes compared to Redfish and Alturas. However, Redfish is the only lake that now supports a sockeye population, and Alturas is the only other lake to have had recent adult sockeye returns (Bowles and Cochnauer 1984). Planned modification of low-water dams on the outflow of Stanley and Pettit Lakes, in addition to possible whole lake fertilization aimed at increasing food availability for juvenile sockeye, makes these lakes attractive for reintroduction of endangered Snake River Sockeye Salmon.

The differences in zooplankton biomass in the lakes may be, in part, due to differences in the abundances of zooplanktivorous fish in each lake. Yellow Belly Lake, with a high zooplankton biomass contains only cutthroat trout that often feed preferentially on benthic invertebrates rather than zooplankton (Luecke 1986). Likewise, Pettit Lake is dominated by brook trout (*Salvelinus fontinalis*), bull trout (*S. confluentus*), stocked rainbow trout (*Oncorhynchus mykiss*), and a small population of redbside shiners (*Richardsonius balteatus*). Stanley Lake has several trout species, redbside shiners, and kokanee salmon (resident *O. nerka*). Both Redfish and Alturas Lakes have large populations of kokanee salmon that may prey on larger zooplankton and depress their abundance. Competition between kokanee salmon and reintroduced sockeye salmon may therefore be an important consideration for recovery of the endangered species.

Additionally, the abundance of piscivorous fishes in the lakes may affect survival of juvenile *O. nerka*. Stanley and Yellow Belly lakes appear to have higher abundances of piscivorous fish than are present in Redfish and Alturas lakes (Spaulding 1993). Consequently, there may well be a trade off between growth potential and mortality due to predators. Additional piscivore assessment and modeling efforts are needed before the tradeoffs between sockeye growth and survival can be properly evaluated for these lakes.

Consideration of both the potential growth and survival of juvenile sockeye salmon is essential before plans to rehabilitate this endangered stock are finalized. Our limnological work has provided a template for future management options and research. Investigations of published sockeye models indicated that our bioenergetics/zooplankton foraging model provided the most reasonable results for this system and that future work should include a more rigorous field test of the model. Our limnological data demonstrates these five lakes are relatively unproductive and suggests that the addition of fertilizer, an approach often used to increase the naturally high sockeye production in British Columbia and Alaskan sockeye lakes (Kyle *et al.* 1993; Stockner 1981, 1992; Stockner and Hyatt 1984), may enhance endangered sockeye salmon growth and thus survival.

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Literature Cited

- Adams, V.D. 1991. Analytical procedures for selected water quality parameters. Utah Water Research Laboratory.
- Ali, M.A. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. *Can. J. Zool.* 37:965-996.
- APHA. 1992. Standard Methods for the examination of water and wastewater. Eds. A.E. Greenberg, L.S. Clesceri, and A.D. Eaton. American Public Health Association, Washington DC.
- Beauchamp, D.A., D.J. Stewart, G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. *Transactions of the American Fisheries Society* 118:597-607.
- Bjornn, T.C., D.R. Craddock, and D.R. Corley. 1968. Migration and survival of Redfish Lake, Idaho, Sockeye Salmon. *Trans. Am. Fish. Soc.* 97:360-373.
- Bowles, E.C. and T. Cochnauer. 1984. Potential sockeye salmon production in Alturas Lake Creek drainage, Idaho. USFS Pub #40-0267-4-127.
- Brett, J. R. 1983. Life Energetics of sockeye salmon, *Oncorhynchus nerka*. In: W. P. Aspey and S.I. Lustric [ed.], *Behavioral Energetics: The cost of Survival in Vertebrates*.
- Brett, J.R. 1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Amer. Zool.* 11:99-113.
- Brett, J.R., S.I. Lustric, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Res. Board Can.* 26:2363-2394.
- Budy, P.B., C. Luecke, W. Wurtsbaugh, and H. Gross. 1993. p.3-28. In Spaulding, S. [ed.] *Snake River Sockeye Salmon (Oncorhynchus nerka) habitat/limnological research*, U.S. Department of Energy, Portland, OR. Project number 91-71. Contract number DE-B179-91BP22548.
- Burgner, R.L. 1992. Life History of sockeye salmon (*Oncorhynchus nerka*), p. 2-117. In C. Groot, L. Margolis [ed.] *Pacific Salmon Life Histories*. University of B.C. Press, B.C., CA.
- Carline, R.F. 1986. Indices as predictors of fish community traits. p. 46-56. In G.E. Hall and M.J. Van Den Avyle [eds.] *Reservoir Fisheries Management: Strategies for the 80's*. reservoir Committee, Southern Division American Fisheries Society, Bethesda.
- Crumpton, W.G. 1987. A simple and reliable method for making permanent mounts of phytoplankton for light and fluorescence microscopy. *Limnol. Oceanogr.* 32:1154-1159.
- Gross, H.P., W.A. Wurtsbaugh, P. Budy, and C. Luecke. 1994. p. 78-97. In D. Teuscher and D. Taki [eds.] *Snake River Sockeye Salmon habitat and limnological research*, U.S. Department of Energy, Portland, OR. Project number 91-71. Contract number DE-B179-91BP22548.
- Gubala, C.P., C. Branch, N. Roundy, D. Landers. 1994. Automated global positioning system charting of environmental attributes: a limnologic case study. *J. Total Environment.* 148(1):83-92.
- Holm-Hansen, O., and B., Riemann. 1978. Chlorophyll-*a* determination: improvements in methodology. *Oikos* 30: 438-447.
- Holmes, R.W. 1962. The preparation of marine phytoplankton for microscopic examination and enumeration on molecular filters. *U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish.* 433, 6 pp.
- Hyatt, K.D. and J.G. Stockner. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. *Can. J. Fish. Aquat. Sci.* 42: 320-331.
- Koenings, J.P. and R.D. Burkett. 1987. Population characteristics of sockeye salmon smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes, p. 216-234. In H.D. Smith, L. Margolis and C.C. Wood (ed.) *Sockeye salmon (Oncorhynchus nerka) population biology and future management*. *Can. Spec. Publ. Fish. Aquat. Sci.* 96.
- Kyle, G.B., J.P. Koenings, and B.M. Barret. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. *Can. J. Fish. Aquat. Sci.* 45:856-867.
- Kyle, G.B., J.P. Koenings, and J.A. Edmundson. 1993. An overview of Alaska lake-rearing enhancement strategy: Nutrient enrichment and juvenile stocking. *In press 1995: Alaskan Freshwaters*.
- Koenings, J.P. and R.D. Burkett. 1987. An Aquatic Rubic's Cube: Restoration of the Karluck Lake Sockeye Salmon (*Oncorhynchus nerka*), p. 419-434. In H.D. Smith, L. Margolis and C.C. Wood (ed.) *Sockeye salmon (Oncorhynchus nerka) population biology and future management*. *Can. Spec. Publ. Fish. Aquat. Sci.* 96.
- LeBrasseur, R.J., C.D. McAlister, W.E. Barraclough, O.D. Kennedy, J. Manzer, and K. Stephens. 1978. Enhancement of sockeye salmon by lake fertilization in Great Central Lake: a summary report. *J. Fish. Res. Bd. Can.* 35:1580-1596.
- Levy, D.A. 1990. Sensory mechanisms and selective advantage for diel vertical migration in juvenile sockeye salmon. *Can. J. Fish. Aquat. Sci.* 47:1796-1802.
- Luecke, C. 1986. Ontogenetic changes in feeding habits of juvenile cutthroat trout. *Trans. Am. Fish. Soc.* 115:703-710.
- McCauley, E. 1984. The Estimation of the Abundance and Biomass of Zooplankton in Samples, Chapter 7, In *A Manual on Methods of Secondary Productivity in Freshwaters*, Second Edition., J.A. Downing and F. Rigler [ed.]. Blackwell Scientific Publishing, Oxford.
- Peterson, J.H. and D.L. DeAngelis. 1992. Functional responses and capture timing in an individual based model: predation by vertebrate squawfish juvenile salmonids in the Columbia River. *Can. J. Fish. Aquat. Sci.* 49: 2551-2565.
- Reynolds, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge.
- Rieman, B.E. and D.L. Meyers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. *Trans. Am. Fish. Soc.* 121:178-191.
- Shortreed, K.S. and J.G. Stockner. 1990. Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. *Can. J. Fish. Aquat. Sci.* 47:262-273.

- Spaulding, S. 1993. Snake River Sockeye Salmon (*Oncorhynchus nerka*) habitat/limnological research. Annual Report 1992. (contract #DE-BI79-91BP22548) to Bonneville Power Administration, Portland, Oregon.
- Stockner, J.G. 1992. Lake fertilization: The enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production, p.199-214, *In* H.D. Smith, L. Margolis and C.C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96:198-215.
- Stockner, J.G. and K.D. Hyatt. 1984. Lake fertilization: state of the art after 7 years of application. Can. Tech. Rep. Fish. Aquat. Sci. 1324: 33 p.
- Stockner, J.G. 1981. Whole-lake fertilization for the enhancement of sockeye salmon (*Oncorhynchus nerka*) in British Columbia, Canada. Internat. Verein. Limnol. Verh. 21:293-299.
- Thorp, J.H. and A.P. Covich. 1991. Ecology and Classification of North American freshwater invertebrates. Academic Press, Inc., San Diego.
- Walters, C.J. DiGisi, J. Post, and J. Sawada. 1991. Kootenay fertilization response model. Fisheries Management Report #98. University of British Columbia, Vancouver.
- Wetzel, R.G. 1983. Limnology. Second Edition. Saunders College Publishing, Philadelphia.

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Environmental Factors Affecting the Western Treehole Mosquito (*Aedes sierrensis*)

Abstract

Water-filled treeholes were investigated to document environmental factors affecting the western treehole mosquito, *Aedes sierrensis*. Waters in northern California treeholes were characterized by relatively high pH, high conductivity, high potassium, and high boron concentrations. Some of the chemical factors (nitrate, chloride and iron) were correlated with emergence of *A. sierrensis*. The physical factors of treehole surface area, number of stems and the amount of organic matter in the treehole also were correlated with the emergence of *A. sierrensis* from treeholes. Interspecific biological interactions, such as predation or competition among aquatic macroinvertebrates, were not found to be important for *A. sierrensis*. Intraspecific competition for limited food resources was important for *A. sierrensis*. Resource limitation might also affect other organisms inhabiting other phytotelmata.

Introduction

Phytotelmata are small aquatic habitats associated with living or dead plants. Water-holding flower bracts, modified leaves, leaf axils or stem internodes are found in at least 29 plant families distributed throughout the world (Fish 1983). Conspicuous phytotelmata include pitcher plants and bromeliad axils. Water-filled treeholes occur over a vast geographic range, largely corresponding to that of hardwood trees. Crotches or rotted limbs or trunks of trees often form cavities which collect rainwater. Treeholes support unusual assemblages of aquatic biota. The treehole water may be very turbid and the treeholes dark. Photosynthetic plankton are rare in these microlentic habitats. Low dissolved oxygen concentrations may further limit the diversity of biota. In California, treehole water may freeze in the winter, and some treeholes dry up by late May (summer rains are rare or absent), so the productive season for aquatic organisms may be brief.

Oligochaetes and acarines occur in treehole waters, but immature insects usually dominate the macroinvertebrate biomass. Throughout the world, mosquitoes are among the most frequent and numerous inhabitants of treeholes (Bradshaw and Holzapfel 1991). Five species of mosquito larvae have been collected from northern California treeholes (D.L.W. unpublished data). According to the classification of Rohnert (1950), two of these species (*Culiseta incidens* and *Culex stigmatosoma*) are dendrolimnetophiles (generalists attracted to a wide variety of aquatic habitats); one (*Aedes increpitus*) is a dendrolimnetoxene (an accidental inhabitant which is not a regular member of the treehole com-

munity); and two (*Orthopodomyia signifera* and *Aedes sierrensis*) are dendrolimnetobionts (organisms largely restricted to treeholes).

Some parasites (e.g., Egerter and Anderson 1985, Washburn *et al.* 1989) and pathogens (e.g., Pinnock *et al.* 1973, Samson and Soares 1984) have been studied more than predators in treeholes of western North America. The role of interspecific competition in western treeholes is not known.

Abiotic factors in western treeholes have not been thoroughly studied. Water chemistry, amount of organic matter in the treehole, physical dimensions and factors relative to the location of a treehole might influence mosquito production directly or by affecting the biotic factors. The importance of interactions among biotic and abiotic factors in affecting larval mosquito populations in phytotelmata is poorly known (Walker *et al.* 1991).

Aedes sierrensis is the most common insect in California treeholes. This species is important because it is a vector of deer bodyworm (*Setaria yehi*) and canine heartworm (*Dirofilaria immitis*) (Weinmann *et al.* 1973, Weinmann and Garcia, 1974). The present study was conducted to investigate physical, chemical, and biological factors associated with some California treeholes and to determine which factors affect the emergence of *A. sierrensis*.

Materials and Methods

Twenty-four trees in nine different areas of Lake and Mendocino counties were included in this study. Species examined included California black oak (*Quercus kelloggii*), interior live oak (*Quercus*

wislizenii), blue oak (*Quercus douglasii*), valley oak (*Quercus lobata*) and Pacific madrone (*Arbutus menziesii*).

According to Munz's (1959) classification of California plant communities, areas K, JM and G are northern oak woodlands and areas HR, EB, WB, MC, RH and HS are foothill woodlands. Areas K and G were the most densely forested sites. Areas HR and MC had the lowest density of trees.

Latitude, longitude and elevation were determined from topographic maps. The direction and angle of slope of the ground were determined with a compass and clinometer. Each study tree was identified (Munz 1959) and its height determined with a clinometer.

All leaves, organic detritus, etc. were removed from each treehole, drained, weighed and recorded as treehole "organic matter." "Treehole volume" was determined by adding known quantities of water to an empty treehole. Water surface area was calculated from multiple width and length measurements. Maximum treehole depth was also measured. The compass direction of the treehole opening (which could influence the amount of leaves, rainwater or sunlight entering a treehole) was recorded.

On 21 February 1985 a water sample was obtained from each treehole and water quality factors were determined according to standard methods (Greenberg 1985). When *A. sierrensis* pupae began to appear, emergence traps (Woodward *et al.* 1988) were placed over 13 treeholes. Twice each week, emerged adults were collected from each trap and identified (Bohart and Washino 1978, Woodward *et al.* 1988). Emergence of *A. sierrensis* typically ceases by August (Garcia *et al.* 1989) so emergence was monitored until 02 September.

The total number of *A. sierrensis* emerging was regressed on various physical, chemical and biological factors (Northwest Analytical 1986). Percentages were transformed to arcsine square roots prior to regression analyses. Differences between tree species (except the two *Q. lobata*) and between slope directions were tested by one-way analysis of variance and Newman-Keuls multiple range tests.

Results and Discussion

The water quality data appear in Table 1. There was relatively little variability in some chemical fac-

tors (e.g., magnesium and nitrate). However other factors showed considerable variability among treeholes. For instance, the maximum potassium concentration (2,610 mg/l) was more than 104 times greater than the minimum concentration (25 mg/l).

Boron concentrations have not been reported in most treehole studies, but the average boron concentration in natural fresh waters is ca. 0.01 parts per million (ppm) (Wetzel 1975). The mean boron concentration in treehole waters of the present study was 0.36 ppm.

Vrtiska and Pappas (1984) found that Nebraska treeholes had water hardness values (mean = 9.3 ppm) significantly lower than waters from other mosquito larval habitats. Water hardness in the present study was relatively high (mean = 113 ppm).

Treehole waters often have high potassium concentrations (Peterson and Chapman 1969, Washburn and Anderson 1986). Vrtiska and Pappas (1984) reported that potassium concentrations (298 ppm) in treehole waters were significantly higher than in other mosquito larval habitats. In the present study the mean potassium concentration was very high (520 ppm).

The mean pH was 7.8 and the mean conductivity was 1,286 μ mhos/cm (Table 1). Kitching (1983) reported a mean pH of 6.4 and a mean conductivity of 339 mS/cm in some European treeholes, and a mean pH of 5.9 and conductivity of 227 mS/cm in Australian treeholes. Vrtiska and Pappas (1984) reported a mean pH of 6.9 and mean conductivity of 456 μ mhos in waters of Nebraska treeholes.

Lunt and Peters (1976) found *Aedes hendersoni* in treehole water with a pH of 9.3, but *Anopheles barberi* larvae were not found in treeholes with a pH greater than 8.7. In a study of Louisiana treeholes (Peterson and Chapman 1969), some larvae (e.g., *Toxorhynchites rutilus septentrionalis*) were collected in water having a pH of 9.9, but the treehole mosquito *Aedes triseriatus* was absent from all treeholes having a pH greater than 8.8. In the present study, *A. sierrensis* larvae were present (in low numbers) in the treehole with the highest pH (8.5 in EB-1).

Peterson and Chapman (1969) found that *A. triseriatus* was absent in treehole waters having electrical conductivities greater than 4,100 μ mhos/cm. Washburn and Anderson (1986) collected *A. sierrensis* larvae from treehole waters and

TABLE 1. Analyses of water samples collected from treeholes in northern California.

Tree	pH (units)	Chemical oxygen demand (mg/l)	Potassium (mg/l)	Electrical conductivity (μ mhos/cm)	Total dissolved solids (mg/l)	Iron (mg/l)	Manganese (mg/l)	Copper (mg/l)	Magnesium (mg/l)	Calcium (mg/l)	Hardness (mg/l)	Nitrate (mg/l)	Chloride (mg/l)	Boron (mg/l)
K-2	7.5	710	240	664	986	0.3	1.70	0.01	11	44	155	0.4	7	0.23
K-4	8.3	390	200	658	756	0.2	0.50	0.01	8	24	93	0.5	5	0.72
K-8	8.2	1340	462	2041	1786	0.5	0.20	0.01	13	20	103	0.6	13	0.37
K-9	8.6	380	350	977	954	0.2	0.80	0.01	10	17	84	0.4	6	0.06
JM-1	6.6	450	33	452	424	0.3	1.20	0.01	6	19	72	0.4	9	0.24
JM-2	7.4	260	27	183	224	0.2	0.20	0.01	3	15	50	0.4	4	0.29
HR-1	7.4	2590	481	1492	2520	0.7	0.50	0.01	7	31	106	0.8	11	0.79
HR-2	8.6	1280	848	1675	2072	0.6	0.50	0.17	9	31	114	0.8	17	0.37
EB-1	8.6	9830	2610	4780	11670	7.0	3.10	0.03	49	64	362	1.0	23	1.63
EB-2	8.7	1900	1460	2771	3544	4.0	1.40	0.03	21	24	146	1.0	17	0.67
WB-1	6.2	630	57	311	832	0.2	0.30	0.03	4	23	74	0.7	7	0.28
MC-1	9.5	1240	657	1203	1656	4.0	0.30	0.04	7	22	84	0.7	8	0.30
RH-1	8.8	4480	1416	2486	830	2.0	1.80	0.20	27	37	204	0.8	29	0.19
HS-1	9.4	3120	1445	5933	6950	4.0	0.40	0.02	20	34	167	1.0	17	0.39
G-1	7.0	310	140	454	420	0.4	0.09	0.01	8	19	80	3.0	2	0.02
G-2	8.0	280	166	413	518	0.3	0.09	0.01	7	23	86	7.0	6	0.25
G-3	8.8	240	317	832	776	0.2	0.04	0.01	15	19	109	0.7	5	0.05
G-4	7.4	610	310	245	720	5.0	0.80	0.02	5	16	61	0.6	6	0.18
G-5	8.1	990	489	913	1430	2.4	1.80	0.01	8	31	110	0.7	19	0.26
G-6	6.7	440	36	187	390	0.9	0.10	0.01	5	23	78	0.7	2	0.13
G-7	6.9	180	25	174	255	0.2	0.30	0.01	6	19	72	7.0	4	0.03
G-8	6.5	1200	129	349	1360	3.0	0.90	0.02	9	40	137	0.8	9	0.31
G-9	6.5	530	58	375	268	1.8	0.70	0.01	4	12	46	0.7	10	0.61
Mean	7.8	1451	520	1286	1797	1.7	0.77	0.03	11	26	113	1.3	10	0.36

electrical conductivities of 70 to 8,370 $\mu\text{mhos/cm}$. This is similar to the conductivity range (174 to 5,933 $\mu\text{mhos/cm}$) of waters harboring *A. sierrensis* in the present study.

Peterson and Chapman (1969) collected *A. triseriatus* larvae in waters having a magnesium concentration as high as 8.6 milligram equivalents per liter and calcium concentration as high as 27.1 milligram equivalents per liter. Washburn and Anderson (1986) found *A. sierrensis* larvae occurred in treeholes with magnesium concentrations as high as 125 ppm and calcium concentrations as high as 258 ppm. In the present study *A. sierrensis* larvae occurred in waters having a magnesium concentration as high as 49 ppm and a calcium concentration as high as 64 ppm. These concentrations of magnesium and calcium are higher than those occurring in most lentic habitats (Wetzel 1975).

Additional factors associated with treeholes appear in Table 2. The mean treehole surface area was 554 cm^2 and the mean depth was 22.2 cm. Kitching (1983) reported a mean surface area of 422 cm^2 and a mean depth of 15.8 cm in Australian treeholes, and a mean surface area of 423 cm^2 and a mean depth of 25.2 cm for some treeholes in England.

The size (volume) of the treehole (Table 2) was not significantly correlated ($P > 0.05$) with the species of tree. *Quercus douglasii* treeholes were significantly ($P < 0.05$) higher above the ground than treeholes in other species. There were no differences ($P > 0.05$) among tree species in treehole depth, treehole surface area or the amount of organic matter in a treehole. There was no correlation ($P > 0.05$) between the height of the tree and the height, depth, surface area, or volume of the treehole.

Some of the ions were positively correlated with each other, so they may have a common source (Table 3). This finding is consistent with reports that stemflow (rain water which runs down the side of a tree) is important in bringing some inorganic ions into treeholes (Fish 1983, Wallace *et al.* 1991).

Emergence traps over selected treeholes (Table 4) collected nine species including a mosquito (*A. sierrensis*), a marsh beetle (*Cyphon* sp.), a moth fly (*Telmatoctopus* sp.), a hover fly (*Blera humeralis*), two midges (*Polypedilum pedatum* and *Limnophyes hamiltoni*) and two biting midges

(*Culicoides neofagineus* and *C. cavaticus*). The emergence of adult male *A. sierrensis* was most highly correlated ($P < 0.01$) with the amount of organic matter in the treehole (Figure 1). The organic matter may include leaf litter, mistletoe and dead organisms which have fallen in the hole, dead moss and lichens which occur near some treeholes, twigs, catkins, acorns, pollen, seeds, etc. Decayed organic matter is an ovipositional attractant for *A. sierrensis* (Ahmadi and McClelland 1983), so the treeholes with greater amounts of organic matter may have had more eggs.

Larvae of some treehole mosquitoes (e.g., *Anopheles plumbeus*, *O. signifera*) feed by filtering suspended particles while hanging from the water surface (Zavortink 1985, Bradshaw and Holzapfel 1991). In addition to filtering, *A. sierrensis* larvae commonly dive to the bottom of the treehole to feed by browsing or gnawing on organic matter or associated microbes. *Aedes sierrensis* might be more successful than other treehole insects (Table 4) partly because it is relatively euryphagous.

There can be large numbers ($> 10,000$) of early instar *A. sierrensis* larvae and very little organic matter in some treeholes. This can result in intraspecific competition for the limited amount of resource available. An inadequate food supply for the larvae may result in smaller adults or in fewer mosquitoes emerging from treeholes. Figure 1 shows that *A. sierrensis* emergence is consistent with the reports that populations of eastern treehole mosquitoes are limited by the amount of available food (Fish and Carpenter 1982, Carpenter 1983). Low per capita resources can result in retarded larval growth, reduced pupal weight, reduced survivorship, reduced pupation success and reduced emergence of some species (Hawley 1985, Bradshaw and Holzapfel 1991).

The emergence of females was negatively correlated with the concentration of chloride ions (Figure 2). The maximum chloride concentration found in a treehole (23 ppm) apparently adversely affected *A. sierrensis* development. Vrtiska and Pappas (1984) indicated tree holes containing *A. triseriatus* were characterized by low chloride (mean = 6.2 ppm) but Peterson and Chapman (1969) collected living *A. triseriatus* larvae in treeholes having chloride concentrations as high as 12.5 milligram equivalents per liter. *Aedes sierrensis* (or some important microbe) may be relatively sensitive to chloride ions.

TABLE 2. Physical and other factors relative to water-filled treeholes in northern California.

Tree	Latitude (North)	Longitude (West)	Elevation (meters)	Slope direction (degrees)	Slope angle (percent)	Tree species	Tree stems (no.)	Tree height (meters)	Treehole direction (degrees)	Treehole height (cm)	Treehole depth (cm)	Surface area (sq cm)	Treehole volume (cc)	Organic matter (grams)
K-2	38°56′	122°47′	563	228	19	<i>Quercus kelloggii</i>	2	17.1	315	9	29.0	210	4150	815
K-4	38°56′	122°47′	566	228	24	<i>Quercus kelloggii</i>	2	13.7	225	0	9.0	198	970	200
K-8	38°56′	122°47′	563	228	16	<i>Quercus kelloggii</i>	4	14.0	235	10	22.0	595	24550	865
K-9	38°56′	122°47′	564	233	19	<i>Quercus kelloggii</i>	3	16.2	54	16	28.0	437	12800	685
JM-1	38°55′	122°46′	651	23	9	<i>Quercus kelloggii</i>	4	20.7	90	80	10.0	630	—	1105
JM-2	38°55′	122°46′	652	113	9	<i>Quercus kelloggii</i>	2	18.6	0	50	9.0	90	1000	105
HR-1	38°59′	122°49′	418	198	3	<i>Quercus douglasii</i>	4	5.9	355	102	2.0	36	730	62
HR-2	38°59′	122°49′	418	198	2	<i>Quercus douglasii</i>	1	7.3	10	510	170.0	516	—	—
EB-1	38°59′	122°40′	436	288	23	<i>Quercus douglasii</i>	5	9.4	270	8	8.0	24	2900	10
EB-2	38°59′	122°40′	436	298	27	<i>Quercus douglasii</i>	3	9.8	300	43	19.5	81	5600	50
WB-1	38°59′	122°41′	411	273	11	<i>Quercus wislizenii</i>	2	14.0	10	50	9.0	96	—	10
MC-1	39°12′	122°55′	475	223	6	<i>Quercus lobata</i>	5	19.8	190	130	42.0	4800	192831	—
RH-1	39°07′	122°54′	430	73	15	<i>Quercus douglasii</i>	3	15.8	125	400	33.0	2097	85163	125
HS-1	38°56′	122°56′	561	118	5	<i>Quercus douglasii</i>	1	17.1	165	200	22.0	—	15740	—
G-1	39°14′	123°06′	330	86	4	<i>Arbutus menziesii</i>	5	12.5	105	9	12.5	442	10200	1570
G-2	39°14′	123°06′	332	95	7	<i>Arbutus menziesii</i>	3	13.1	240	5	7.0	570	3200	1340
G-3	39°14′	123°06′	332	95	7	<i>Arbutus menziesii</i>	2	13.4	285	5	12.0	160	650	100
G-4	39°14′	123°06′	333	27		<i>Quercus wislizenii</i>	2	14.3	260	5	7.0	144	960	170
G-5	39°14′	123°06′	332	12	6	<i>Quercus wislizenii</i>	2	16.5	130	9	6.0	126	700	260
G-6	39°14′	123°06′	333	50	17	<i>Quercus wislizenii</i>	5	15.5	135	24	11.0	294	4600	950
G-7	39°14′	123°06′	333	53	16	<i>Quercus wislizenii</i>	5	16.2	—	75	28.0	475	12555	1540
G-8	39°14′	123°06′	332	51	21	<i>Quercus wislizenii</i>	2	4.9	87	30	4.0	36	390	100
G-9	39°14′	123°06′	332	55	22	<i>Quercus wislizenii</i>	3	15.7	163	20	4.0	144	—	—
Mean			441	141	13		3	14.0	163	77	22.2	554	19983	529

TABLE 3. Matrix of Spearman's rank correlation coefficients (ρ) of physical and chemical measurements of 13 water-filled treeholes.

	Volume	Surface area	Depth	pH	Conduc- tivity	T.D.S.	C.O.D.	Nitrate	Iron	Manga- nese	Copper	Magne- sium	Calcium	Hard- ness	Chlo- ride	Boron	Potas- sium
Organic mat.	.438	.897**	.353	-.526	-.438	-.587*	-.460	-.288	-.361	-.251	-.360	-.371	-.309	-.466	-.530	-.620*	-.501
Volume		.543	.725**	.273	.165	-.027	.099	.082	-.011	.129	.132	.152	-.155	-.110	-.102	-.033	.010
Surface area			.620*	-.345	-.262	-.507	-.507	-.326	-.485	-.299	-.338	-.135	-.424	-.419	-.532	-.592*	-.370
Depth				.356	.231	-.022	-.121	-.099	-.418	-.052	-.088	.323	-.144	.071	-.192	-.203	.022
pH					.672*	.540	.441	.088	-.032	.576*	.335	.477	.363	.471	.456	.669*	.565*
Conductivity						.907**	.703**	.420	.313	.514	.409	.790**	.526	.725**	.813**	.571*	.923**
T.D.S.							.890**	.453	.571*	.508	.591*	.707**	.655*	.786**	.934**	.654*	.885**
C.O.D.								.412	.709**	.525	.610*	.433	.694**	.615*	.852**	.731**	.687**
Nitrate									.536	-.065	.549	.393	.265	.357	.269	.104	.398
Iron										.418	.827**	.221	.383	.352	.599*	.286	.495
Manganese											.420	.224	.468	.434	.650*	.456	.659*
Copper												.522	.409	.519	.582*	.478	.500
Magnesium													.497	.828**	.593*	.301	.641*
Calcium														.845**	.637*	.537	.433
Hardness															.728**	.401	.632*
Chloride																.665*	.852**
Boron																	.489

* $P < 0.05$ ** $P < 0.01$

TABLE 4. Mean numbers of insects collected per trap per night in emergence traps from 28 March to 02 September 1985.

Tree	<i>Cyphon</i> sp.	<i>Telmatoscopus</i> sp.	<i>Blera</i> <i>humeralis</i>	<i>Limnophyes</i> <i>hamiltoni</i>	<i>Polypedilum</i> <i>pedatum</i>	<i>Culicoides</i> <i>cavaticus</i>	<i>Culicoides</i> <i>neofagineus</i>	<i>Aedes sierrensis</i>		
								♀ ♀	♂ ♂	total
K-2	0.08	0.06	0.00	0.01	0.00	0.00	0.10	0.06	0.04	0.10
K-4	0.00	0.10	0.04	0.00	0.00	0.13	0.06	0.61	0.62	1.23
K-8	0.35	0.09	0.00	0.00	0.00	0.16	0.15	0.98	2.38	3.36
J-2	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.39	0.25	0.64
H-1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	2.00	2.88
EB-1	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.03	0.02	0.05
EB-2	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.06	0.03	0.09
G-1	0.00	0.03	0.01	0.02	1.88	0.11	0.00	3.11	5.37	8.48
G-3	0.00	0.11	0.01	0.03	0.00	0.10	0.00	0.04	0.04	0.08
G-4	0.00	0.00	0.01	0.01	0.00	0.02	0.00	0.03	0.00	0.03
G-5	0.00	0.00	0.06	0.04	0.00	0.18	0.02	0.49	0.16	0.65
G-6	0.00	0.00	0.00	0.01	0.00	0.16	0.01	3.95	4.99	8.94
G-8	0.00	0.07	0.00	0.00	0.00	0.57	0.01	0.55	0.73	1.28
Mean	0.03	0.04	0.01	0.01	0.14	0.12	0.03	0.86	1.28	2.14

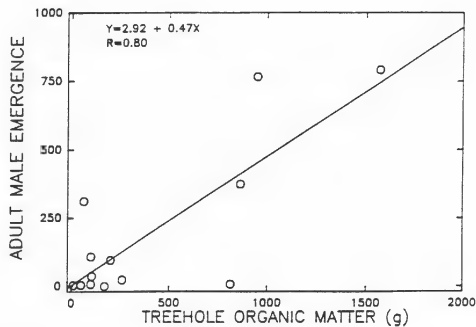


Figure 1. Relationship between the amount of organic matter in California treeholes and emergence of adult male *Aedes sierrensis*.

It has been suggested that some mosquitoes in phytotelmata experience delays in larval development times and a sex ratio distorted in favor of males. When larval resources are scarce there could be reduced production of adult females, the heavier and more expensive sex, and the reduction might serve as a feedback mechanism to regulate population size (Frank *et al.* 1985). In the present study females constituted only 40.1% of the emerged adults, but there was no significant correlation between sex ratio and amount of organic matter in the treehole. Female *A. sierrensis* emerge later than males (Garcia *et al.* 1989), so deeper treeholes might be expected to be better

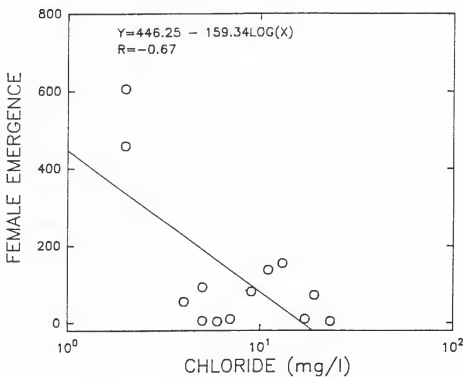


Figure 2. Relationship between the chloride concentration in treehole waters and the emergence of adult female *Aedes sierrensis* from northern California treeholes.

suited for the females. However there was no correlation between treehole depth and percentage of females emerging from treeholes.

Of the factors in Tables 1-4, the percentage of females was positively correlated only with the concentration of iron in the treehole water (Figure 3). Iron may not be immediately toxic to *A. sierrensis* larvae, but can have complicated affects on other factors including nitrogen, chloride, phosphorous, pH, redox potential, primary production, and bacterial metabolism (Wetzel 1975).

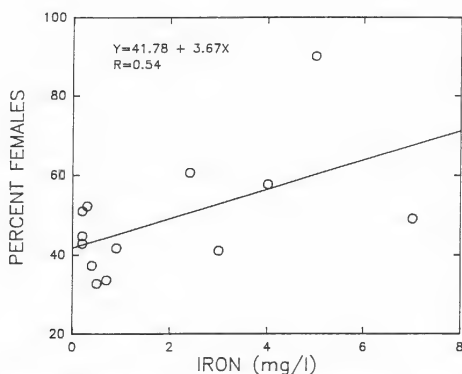


Figure 3. Relationship between the iron concentration in tree-hole waters and the percentage of adult female *Aedes sierrensis*.

The total adult *A. sierrensis* emergence also was compared with chemical, physical and biological factors in Tables 1-4. Cadavers of other organisms might serve as food for *A. sierrensis* larvae. Of the insects in these treeholes, only the *Culicoides* are considered to be possible predators (Merritt and Cummins, 1984). Other treehole insects could be considered as possible competitors of *A. sierrensis*. However, there were no significant correlations ($P > 0.05$) between the emergence of *A. sierrensis* and the emergence of any of the other species in Table 4, so interspecific biological interactions were not found to be important for *A. sierrensis*. Also the number of insect species per treehole was not correlated with *A. sierrensis* emergence.

Larval predators (e.g., *Toxorhynchites* mosquitoes or cyclopoid copepods) can reduce some populations of treehole mosquitoes (Bradshaw and Holzapfel 1984, Riviere *et al.* 1987). However these predators are rare or absent in California treeholes.

The lower elevation treeholes were in hotter, drier areas and may have dried out sooner than the higher elevation treeholes. However the *A. sierrensis* in the lower treeholes may have started emerging sooner than the higher elevation mosquitoes, and there was no ($P < 0.05$) significant correlation between number of adults emerging and elevation. There was no correlation between slope angle and *A. sierrensis* emergence. The number of mosquitoes emerging was highest ($P < 0.05$) on south-facing ($121-240^\circ$) slopes, which are commonly hot and dry in California. Bradshaw and Holzapfel (1991) reported higher survivorship of a treehole mosquito (*A. plumbeus*) on south-facing slopes in England.

Non-deciduous trees (e.g., interior live oak and madrone) may produce more of the chemicals that deter herbivores when compared to deciduous oaks because evergreen leaves are vulnerable all year. High concentrations of tannins and lignins reportedly make *Q. wislizenii* less palatable and less nutritious to insects and mammals (Pavlik *et al.* 1991). Tannins produced by some species of trees may have effects on *A. sierrensis* larvae or their natural enemies (Mercer and Anderson 1994). However in the present study there were no significant differences between tree species in the number of adult mosquitoes emerging or their sex ratios.

Treeholes high in trees may receive nutrients from flying organisms and from wind-borne material (anemophilous nutrition). Lower treeholes may also receive acorns and other materials falling into the water or washed by rainwater into the treehole (dendrophilous nutrition according to Frank 1983). The height of the treehole is important for some mosquito species (Sinsko and Grimstad 1977). There was no significant correlation between treehole height and *A. sierrensis* emergence, but treeholes on the highest limbs were not sampled in this study.

Copeland and Craig (1990) found *A. triseriatus* in more shallow treeholes and fewer deep treeholes than expected, and the reverse was true for *Orthopodomyia alba*. In the present study the numbers of emerged *A. sierrensis* were not correlated ($P > 0.05$) with treehole depth.

Total emergence was not correlated with latitude, longitude, or height of tree, but was correlated with the number of major stems (Figure 4).

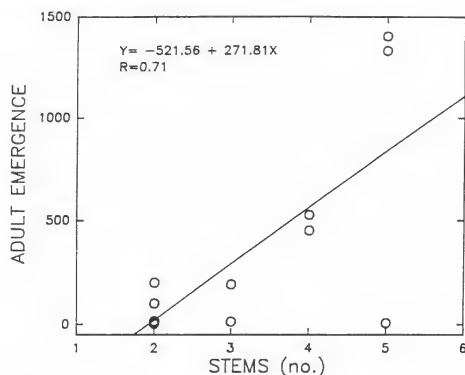


Figure 4. Relationship between the number of major trunk stems on a hardwood tree and the total emergence of adult *Aedes sierrensis* from northern California treeholes.

Some of the trees in this study apparently had been cut to near ground level years ago. The old stump may have become the bottom of a treehole when several trunks sprouted around its circumference. The multiple trunks might funnel stemflow, falling leaves, etc. into these basal treeholes.

Lunt and Peters (1976) found *O. alba* only in treeholes with narrow openings (1.5-1.7 cm). They indicated the surface area of the treehole apparently was not important for *A. hendersoni* or *A. triseriatus*.

The total emergence of *A. sierrensis* was positively correlated with three possibly associated factors: surface area, organic matter, and nitrate (Figure 5). The surface area was positively correlated ($P < 0.05$) with the amount of organic matter in the treehole (Table 3). A treehole with a larger opening would probably have more leaves and other materials falling into it so it would therefore have a greater accumulation of organic matter than treeholes with smaller surface areas. Water with greater organic loading could have greater nitrate concentrations. Nitrate was significantly ($P < 0.05$) correlated with the amount of organic matter in the treehole (Table 3). However, some nitrate also enters treeholes via stemflow. Nitrate can stimulate microbial respiratory metabolism and growth, and detritus decomposition on leaf and bark surfaces and in the water column, thereby providing more mosquito food (Walker *et al.* 1991). Figure 5 is consistent with the finding of Carpenter (1982) that mosquito growth was enhanced in microcosms enriched with nitrate.

The organic matter in many treeholes is largely leaves, which can be used for rearing *A. sierrensis* (Pyle *et al.* 1989). Parts of leaves may be directly ingested by mosquito larvae, or may indirectly provide nourishment through decomposers. Biological transformation of organic matter may be important in treeholes. Fungi are decomposers which can be ingested by treehole mosquito larvae. Carpenter (1983) has shown that leaves in water without mosquito larvae develop massive hyphal growths, but leaves in the presence of eastern treehole mosquito larvae are nearly free of fungi. This is reportedly due to browsing by the larvae. Some protozoans, bacteria and other microorganisms on the leaves may also be ingested by treehole mosquito larvae.

It should be noted that nonaquatic organisms may alter the leaves and other organic matter

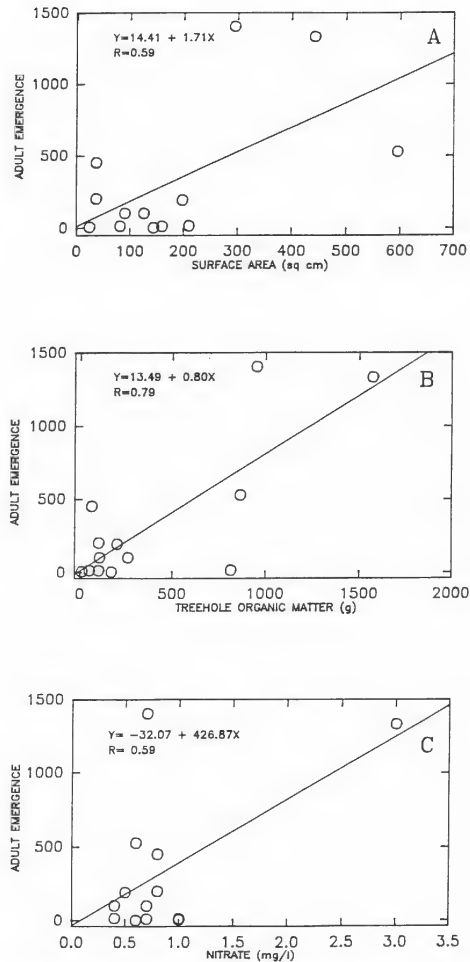


Figure 5. Relationship between treehole surface area (A), treehole organic matter (B), and concentration of nitrate in treehole water (C), and the emergence of adult *Aedes sierrensis*.

when California treeholes are dry in the late summer and early autumn. The leaves and organic matter then provide habitat for numerous invertebrate and vertebrate species (Pavlik *et al.* 1991). The partial processing of the leaves as well as the exuviae, dead organisms, feces, etc. in the treeholes when they are flooded by winter rains may affect the mosquito productivity of a treehole.

The association of emergence with the amount of organic matter in treeholes is consistent with the

idea that treehole mosquito populations are often limited by the larval food supply (Bradshaw and Holzapfel 1991). Eggs, pupae and adults do not feed on the treehole organic matter so the larval stage is the limiting one.

Walker and Merritt (1988) found no difference in the number of *A. triseriatus* emerged from treeholes without leaves or treeholes with leaves. However, emergence of *A. sierrensis* is affected by the amount of leaf litter. Figure 5 is consistent with the idea that *A. sierrensis* is food limited (Gilpin and Langford 1978). Even those adults which do emerge from food-limited phytotelmata may exhibit relatively small size, low survivorship, or low fecundity (Hawley 1985, Bradshaw and Holzapfel 1992).

There are other possible environmental factors which could impact *A. sierrensis*. Some parasites and pathogens have been examined extensively (e.g., Sanders 1972; Sanders and Poinar 1976; Soares 1982; Hawley 1985; Washburn and Anderson 1986; Saunders *et al.* 1988; Washburn *et al.* 1988a, 1988b, 1991; Norton *et al.* 1992) and were not further evaluated in the present study. Interspecific competition may be important in treeholes having higher densities of organisms than in the present study. Also factors which could affect eggs before they contact the water (e.g., predation by ants) or adults after they leave a treehole

(Washburn 1991) were not examined in this study. It is possible that there are water-filled cavities in the center of a tree or very high on limbs which were not found for this study. For eggs hatching after the fall, intermittent drying or freezing can affect the larval development. Heavy rains can wash out eggs, larvae, nutrients or waste products (Walker *et al.* 1991, Washburn and Anderson 1993). Furthermore, some of the factors (e.g., hydrochemical conditions) may change considerably during the course of a season. The factors which limit mosquito production in a treehole may change between high rainfall years and drought years. For these reasons, the results of this study should not be overgeneralized. The roles of possible indirect or interacting biotic and abiotic factors (e.g., number of stems and treehole surface area may affect stemflow which may alter concentrations of nitrate or iron or tannins which may influence bacteria or fungi which may affect food availability for macroinvertebrates) warrant further research. Additional studies are also needed to determine the roles of chemical, biological and physical factors in phytotelmata in other regions.

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Literature Cited

- Ahmadi, A., and G. A. H. McClelland. 1983. Oviposition attractants of the western treehole mosquito *Aedes sierrensis*. Mosq. News 43:343-345.
- Bohart, R. M., and R. K. Washino. 1978. Mosquitoes of California. University of California, Berkeley, CA. 153 p.
- Bradshaw, W. E., and C. M. Holzapfel. 1984. Seasonal development of tree-hole mosquitoes (Diptera: Culicidae) and Chaoborids in relation to weather and predation. J. Med. Entomol. 21:366-378.
- . 1991. Fitness and habitat segregation of British treehole mosquitoes. Ecol. Entomol. 16:133-144.
- . 1992. Reproductive consequences of density-dependent size variation in the pitcher plant mosquito, *Wyeomyia smithii* (Diptera: Culicidae). Ann. Ent. Soc. Am. 85:274-281.
- Carpenter, S. R. 1982. Stemflow chemistry: effects on population dynamics of detritivorous mosquitoes in tree-hole ecosystems. Oecologia 55:1-6.
- . 1983. Resource limitation of larval treehole mosquitoes subsisting on beech detritus. Ecology 64:219-223.
- Copeland, R. S. and G. B. Craig, Jr. 1990. Habitat segregation among treehole mosquitoes (Diptera: Culicidae) in the Great Lakes region of the United States. Ann. Ent. Soc. Am. 86:1063-1073.
- Egarter, D. E. and J. R. Anderson. 1985. Infection of the western tree hole mosquito, *Aedes sierrensis* (Diptera: Culicidae) with *Lambornella clarki* (Ciliophora: Tetrahymenidae). J. Invert. Pathol. 46:296-304.
- Fish, D. and S. R. Carpenter. 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. Ecology 63:283-288.
- Fish, D. 1983. Phytotelmata: Flora and fauna. In: J. H. Frank and L. P. Lounibos (eds.) Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing, Medford, NJ. Pp. 1-28.
- Frank, J. H. 1983. Bromeliad phytotelmata and their biota, especially mosquitoes. In: J. H. Frank and L. P. Lounibos (eds.) Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing, Medford, NJ. Pp. 101-128.
- Frank, J. H., G. A. Curtis and J. T. Richard. 1985. Density dependent sex ratio distortion and developmental bimodality in *Wyeomyia vanduzeei*. In: L. P. Lounibos, J. R. Rey and J. H. Frank (eds.) Ecology of Mosquitoes: Proceedings of a Workshop. Florida Medical Entomology Laboratory, Vero Beach, FL. Pp. 155-166.
- Garcia, R., A. E. Colwell, W. G. Voigt, and D. L. Woodward. 1989. Fay-Prince trap baited with CO₂ for monitoring adult abundance of *Aedes sierrensis* (Diptera: Culicidae). J. Med. Entomol. 26:327-331.

- Greenberg, A. E. (ed.) 1985. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Washington, DC. 1268 p.
- Gilpin, M. E., and R. P. Langford. 1978. Evidence for density dependent growth regulation among larval *Aedes sierrensis* mediated by food competition. Proc. Calif. Mosq. Vector Cont. Assoc. 46:42-45.
- Hawley, W. A. 1985. Population dynamics of *Aedes sierrensis*. In: L. P. Lounibos, J. R. Rey and J. H. Frank (eds.). Ecology of Mosquitoes: Proceedings of a Workshop. Florida Medical Entomology Laboratory, Vero Beach, FL. Pp. 167-184.
- Jenkins, D. W. and S. J. Carpenter. 1946. Ecology of the tree hole breeding mosquitoes of Nearctic North America. Ecol. Monographs 16:32-47.
- Kitching, R. L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. J. Animal Ecol. 40:281-302.
- . 1983. Community structure in water-filled treeholes in Europe and Australia—comparisons and speculations. In: J. H. Frank and L. P. Lounibos (eds.) Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing, Medford, NJ. Pp. 205-222.
- Kitching, R. L. and C. Callaghan. 1981. The fauna of water-filled treeholes in a box forest in southeast Queensland. Aust. Entomol. Mag. 8:61-70.
- Lounibos, L. P. 1983. The mosquito community of treeholes in subtropical Florida. In: J. H. Frank and L. P. Lounibos (eds.) Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing, Medford, NJ. Pp. 223-246.
- . 1985. Interactions influencing production of tree hole mosquitoes in south Florida. In: L. P. Lounibos, J. R. Rey and J. H. Frank (eds.) Ecology of Mosquitoes: Proceedings of a Workshop. Florida Medical Entomology Laboratory, Vero Beach, FL. Pp. 65-77.
- Lunt, S. R. and C. E. Peters. 1976. Distribution and ecology of tree-hole mosquitoes along the Missouri and Platte Rivers in Iowa Nebraska, Colorado, and Wyoming. Mosq. News 36:80-84.
- Mercer, D. R. and J. R. Anderson. 1994. Tannins in treehole habitats and their effects on *Aedes sierrensis* (Diptera: Culicidae) production and parasitism by *Lambornella clarki* (Ciliophora: Tetrahymenidae). J. Med. Entomol. 31:159-167.
- Merritt, R. W. and K. W. Cummins. 1984. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Dubuque, IA. 722 p.
- Munz, P. A. 1959. A California Flora. Univ. Calif. Press, Berkeley, CA. 1681 p.
- Northwest Analytical. 1985. NWA Statpak multi-function statistics library, version 4.1. Northwest Analytical, Inc., Portland, OR. 570 p.
- Norton, A. J., O. Washburn, and E. M. Omi. 1992. Axenic culture of *Lambornella clarki* (Ciliophora: Tetrahymenidae), an endoparasite of *Aedes sierrensis* (Diptera: Culicidae). J. Invert. Pathol. 60:164-170.
- Papineau, E. A. 1984. Controlling *Aedes sierrensis* in Jackson County, a year-round program. Proc. Calif. Mosq. Contr. Assoc. 52:63-67.
- Pavlik, B. M., P. C. Muick, S. Johnson and M. Popper. 1991. Oaks of California. Cachuma Press, Los Olivos, CA. 184 p.
- Peterson, J. J. and H. C. Chapman. 1969. Chemical factors in tree holes and related breeding of mosquitoes. Mosq. News 29:29-36.
- Pinnock, D. E., R. Garcia and C. M. Cubbin. 1973. *Beauveria tenella* as a control agent for mosquito larvae. J. Invert. Pathol. 22:143-147.
- Pyle, C. A., A. E. Colwell, and D. L. Woodward. 1989. Feeding and survival of laboratory *Aedes sierrensis* larvae. Proc. Calif. Mosq. Vect. Contr. Assoc. 57:56-60.
- Reeves, W. C. 1941. The genus *Orthopodomyia* Theobald in California. Pan-Pac. Entomol. 17:69-72.
- Riviere, F., B. H. Kay, J. M. Klein, and Y. Sechan. 1987. *Mesocyclops aspericornis* (Copepoda) and *Bacillus thuringiensis* var. *israelensis* for the biological control of *Aedes* and *Culex* vectors (Diptera: Culicidae) breeding in crab holes, treeholes and artificial containers. J. Med. Entomol. 24:424-430.
- Roback, S. S. 1974. Insects (Arthropoda: Insecta). In: C. W. Hart and S. L. H. Fuller (eds.) Pollution Ecology of Freshwater Invertebrates. Academic Press, NY. Pp. 313-376.
- Samson, R. A., and G. G. Soares, Jr. 1984. Entomopathogenic species of the hyphomycete genus *Tolypocladium*. J. Invert. Pathol. 43:133-139.
- Sanders, R. D. 1972. Microbial mortality factors in *Aedes sierrensis* populations. Proc. Calif. Mosq. Contr. Assoc. 40:66-68.
- Sanders, R. D., and G. O. Poinar, Jr. 1976. Development and fine structure of *Pleistophora* sp. (Cnidospora: Microsporidia) in the mosquito *Aedes sierrensis*. J. Invert. Pathol. 28:109-119.
- Saunders, G. A., J. O. Washburn, J. R. Anderson and D. E. Egerter. 1988. Pathogenicity of fungi isolated from field-collected larvae of the western treehole mosquito, *Aedes sierrensis* (Diptera: Culicidae). J. Invert. Pathol. 52:360-363.
- Sinsko, M. J., and P. R. Grimstad. 1977. Habitat separation by differential vertical oviposition of two treehole *Aedes* in Indiana. Environ. Entomol. 6:485-487.
- Snow, W. E. 1958. Stratification of arthropods in a wet stump cavity. Ecology 39:83-88.
- Soares, G. C. 1982. Pathogenesis of infection by the hyphomycetous fungus *Tolypocladium cylindrosporum* Gams in *Aedes sierrensis* Ludlow and *Culex tarsalis* Coquillett (Diptera: Culicidae). Entomophaga 27: 283-300.
- Vrtiska, L. A., and L. G. Pappas. 1984. Chemical analysis of mosquito larval habitats in southeastern Nebraska. Mosq. News 44:506-509.
- Walker, E. D., and R. W. Merritt. 1988. The significance of leaf detritus to mosquito (Diptera: Culicidae) productivity from treeholes. Environ. Entomol. 17:199-206.
- Walker, E. D., D. L. Lawson, R. W. Merritt, W. T. Morgan, and M. J. Klug. 1991. Nutrient dynamics, bacterial populations, and mosquito productivity in tree hole ecosystems and microcosms. Ecology 72:1529-1546.
- Washburn, J. O., and J. R. Anderson. 1986. Distribution of *Lambornella clarki* (Ciliophora: Tetrahymenidae) and other mosquito parasites in California treeholes. J. Invert. Pathol. 48:296-309.
- . 1993. Habitat overflow, a source of larval mortality for *Aedes sierrensis* (Diptera: Culicidae). J. Med. Entomol. 30:802-804.

- Washburn, J. O., M. E. Gross, D. R. Mercer, and J. R. Anderson. 1988. Predator-induced trophic shift of a free-living ciliate: parasitism of mosquito larvae by their prey. *Science* 240:1193-1195.
- Washburn, J. O., D. E. Egerter, J. R. Anderson, and G. A. Saunders. 1988. Density reduction in larval mosquito (Diptera: Culicidae) populations by interactions between a parasitic ciliate (Ciliophora: Tetrahymenidae) and an opportunistic fungal (Oomycetes: Pythiaceae) parasite. *J. Med. Entomol.* 25:307-314.
- Washburn, J. O., J. R. Anderson, and D. R. Mercer. 1989. Emergence characteristics of *Aedes sierrensis* (Diptera: Culicidae) from California treeholes with particular reference to parasite loads. *J. Med. Entomol.* 26:173-182.
- . 1991. Parasitism of newly-hatched *Aedes sierrensis* (Diptera: Culicidae) larvae by *Lambornella clarki* (Ciliophora: Tetrahymenidae) following habitat flooding. *J. Invert. Pathol.* 58:67-74.
- Wetzel, R. G. 1975. *Limnology*. W. B. Saunders Co., Philadelphia, PA. 743 p.
- Weinmann, C. J., J. R. Anderson, W. M. Longhurst, and G. Connolly. 1973. Filarial worms of Columbian black-tailed deer in California. I. Observations in the vertebrate host. *J. Wildlife Dis.* 9:213-220.
- Weinmann, C. J., and R. Garcia. 1974. Canine heartworm in California, with observations on *Aedes sierrensis* as a potential vector. *Calif. Vector Views* 21:45-50.
- Woodward, D. L., A. E. Colwell, and N. L. Anderson. 1988. The aquatic insect communities of tree holes in northern California oak woodlands. *Bull. Soc. Vector Ecol.* 13:221-234.
- Zavortink, T. J. 1985. Observations on the ecology of treeholes and treehole mosquitoes in the southwestern United States. pp. 473-487. *In*: L. P. Lounibos, J. R. Rey, and J. H. Frank (eds.) *Ecology of Mosquitoes: Proceedings of a Workshop*, Vero Beach, FL. Pp. 473-487.

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Sequence Analysis of Mitochondrial DNA Variation in *Daphnia*

Abstract

Estimates of mitochondrial DNA sequence variability were determined for two closely related species of *Daphnia*. Sequence analysis from two genes, NADH dehydrogenase subunits 4 and 5, revealed a pattern of nucleotide substitution that has a 10 to 1 transition bias. This pattern is consistent with that from other taxa, suggesting the existence of a universal transition bias. Estimates of nucleotide diversity within species were similar to those obtained from other species. The estimated level of amino acid diversity between *Daphnia* and *Drosophila* was approximately as predicted from molecular clock analyses. Estimates of mitochondrial DNA variability among populations were similar for sequence data and restriction site data, suggesting that restriction endonuclease analyses provide accurate estimates of population-level genetic variability.

Introduction

Advances in sequencing technologies over the past decade (Sanger *et al.* 1977) have provided evolutionary biologists with a remarkable tool for assaying genetic variability. Since its inception, DNA sequencing has been used as a molecular approach for inferring phylogenetic relationships among species. However, only recently has DNA sequencing been used to examine genetic variation at or below the species level (see Hillis *et al.* 1991 for a review). One molecule that has received considerable attention is animal mitochondrial DNA (mtDNA).

Animal mtDNA is a relatively small (~14-16 kilobases), covalently closed circular molecule that is maternally inherited without recombination. These properties, along with its supposedly high rate of evolution (Brown *et al.* 1979), have led to its widespread use in evolutionary studies. Brown *et al.* (1982) proposed that transitions (G <-> A, T <-> C) are strongly favored over transversions (G <-> C, G <-> T, A <-> T, A <-> C) in mitochondrial evolution, despite the neutral prediction which suggests that there should be twice as many transversions as transitions based upon their probability of occurrence (eight ways for transversions to occur, four ways for transitions). Brown *et al.* (1982) showed that in closely related primates, 92% of the nucleotide substitutions are transitions. However, in comparison to more distantly related taxa, this transition bias disappears. Apparently, this transition bias is the result of multiple substitutions replacing transitions as transversions (Brown *et al.* 1982; De Salle *et al.* 1987).

The strong transition bias between closely related taxa is also supported with data from rodents (Brown

and Simpson 1982; Kocher *et al.* 1989), birds (Edwards and Wilson 1990), fish (Thomas and Beckenbach 1989), sea urchins (Giorgi *et al.* 1991), nematodes (Thomas and Wilson 1991), and planarians (Bessho *et al.* 1992). However, data from *Drosophila* (Clary and Wolstenholme 1987) suggest that this transition bias may not occur all taxonomic groups. In fact, in *Drosophila* there is a slight bias towards transversions that is very close to the theoretical expectation (but see De Salle *et al.* 1987). The lack of a transition bias in *Drosophila* is most likely the result of the comparison of *D. yakuba* with *D. melanogaster*, which are not very closely related. In fact, when more closely related species of *Drosophila* are compared, the bias becomes more evident (Beckenbach *et al.*, 1993). Since the majority of the data supporting the existence of a bias have come from vertebrates (mammals in particular) or *Drosophila*, the hypothesis of a widespread transition bias needs to be confirmed with data from other protostomate invertebrates.

Mitochondrial DNA (mtDNA) is known to be variable both within and between species (Moritz *et al.* 1987). The amount of mtDNA variability within species tends to be high. For example, Wayne *et al.* (1991) recently reported up to 8% nucleotide divergence within a single population of black-backed jackals. Between-population estimates of divergence can sometimes approach ten percent (Avise *et al.* 1987). These observations are in agreement with predictions from molecular clock analysis. Calibration of mtDNA molecular clocks for protein-coding genes predicts significant levels of divergence at zero divergence time (i.e., within species), suggesting the potential for high levels of site-specific heterozygosity (Lynch and Jarrell,

¹Current address: Department of Natural Sciences, Longwood College, Farmville, VA 23909

1993). However, some species with large dispersal capabilities or those that have suffered recent bottlenecks may show low levels of diversity (Avise *et al.* 1987).

Daphnia are protostomate, freshwater microcrustaceans that inhabit temporary ponds and permanent lakes over much of Europe and North America. Restriction-site studies (Crease *et al.* 1990), reveal that *Daphnia* exhibit significant amounts of variability for mtDNA both within and between populations. In this manuscript, I report on the pattern of nucleotide substitution within and between two species of *Daphnia* and provide estimates of locus-specific nucleotide diversity for portions of the NADH dehydrogenase subunits 4 and 5 (ND4, and ND5) genes. Data on mtDNA sequence variability in *Daphnia* provide valuable insights about the pattern of nucleotide substitution and also allow estimates of variability obtained from sequencing and restriction-site analysis to be compared. Jarrell (submitted) has shown that estimates of variability from restriction endonuclease analyses tend to be lower than estimates of variability measured from sequence data. Finally, these data for within-species levels of locus-specific heterozygosity can be used to test the prediction that significant levels of baseline heterozygosity should be present for certain loci and should be positively correlated with the rate of evolution of these genes.

Materials and Methods

Field Sampling and Collection Localities

Samples were taken from seven *Daphnia pulex* populations (FC19, FC23, 17, TSP, PA, BUS, and AMZ) and four *Daphnia pulicaria* populations (ODL, LCU, KLA, and HOS); (see Table 1 for a complete description of the populations). One individual was isolated from each of the eleven samples, placed in conditions that favor ameiotic parthenogenesis (Lynch 1983), and allowed to multiply until enough individuals were present to provide an adequate amount of tissue for DNA manipulation. The accumulated individuals were placed into 1.5 ml eppendorf tubes and kept at -80° Celsius prior to DNA isolation. One randomly chosen clonal isolate per population was used for further study.

DNA Extraction and Cloning

Following the procedure of Crease *et al.* (1989), approximately 100 μ g of *Daphnia* tissue (wet

TABLE 1. Sampling Localities of *Daphnia* Populations.

Population	Location	Habitat
<i>D. pulex</i>		
PA	Warren Co., IN	Temporary
TSP	Vermilion Co., IL	Temporary ¹
BU	Champaign Co., IL	Temporary
AM	Lane Co., OR	Temporary
FC19	Essex Co., Ontario, Canada	Temporary
FC23	Essex Co., Ontario, Canada	Temporary
17	Essex Co., Ontario, Canada	Temporary
<i>D. pulicaria</i>		
ODL	Klamath Co., OR	Permanent
LCU	Deschutes Co., OR	Permanent
HOS	Deschutes Co., OR	Permanent
KLA	Klamath Co., OR	Permanent

¹Although the pond was permanent, there was an annual extinction of the *Daphnia* population each fall followed by re-population in the spring.

weight, whole animals) was ground in 400 μ l of a solution containing 0.1 M NaCl, 30 mM Tris (pH 8.0), 10 mM EDTA, 10 mM β -mercaptoethanol, and 0.5% Triton X-100, and subjected to two rounds of phenol extraction followed by two rounds of chloroform:IAA (24:1) extraction. DNA was precipitated by the addition of 0.1 volumes 2M NaCl and 2.5 volumes 100% ethanol, and then resuspended in doubly distilled water.

A genomic DNA library was constructed for each of the eleven individuals by ligation of ~ 0.5 μ g of *Bam*HI digested genomic DNA with 1 μ g of pre-digested lambda phage (Promega Packagene system). *E. coli* MM294 were infected with the recombinant phage and plated onto LB plates. Recombinant clones were screened for the presence of mtDNA inserts by plaque hybridization techniques (Maniatis *et al.* 1982) using radiolabelled *Daphnia* mtDNA (Stanton *et al.* 1991).

Previous analyses of *Daphnia* mtDNA had established that part of the ND4 gene and part of the ND5 gene were at opposite ends of a 1.5 kb *Apa*I-*Sst*I fragment (Figure 1; Crease *et al.* 1990). The desired subclones were produced by ligation of the these fragments into pBS vector. One μ g of each mtDNA recombinant was digested with *Apa*I plus *Sst*I. 0.2 μ g of pBS vector was digested with the same complement of enzymes to produce compatible ends, and treated with phosphatase to prevent self-ligation. In both cases, the enzymes (restriction enzymes and phosphatase) were removed by extraction with phenol. After ethanol

Daphnia pulex

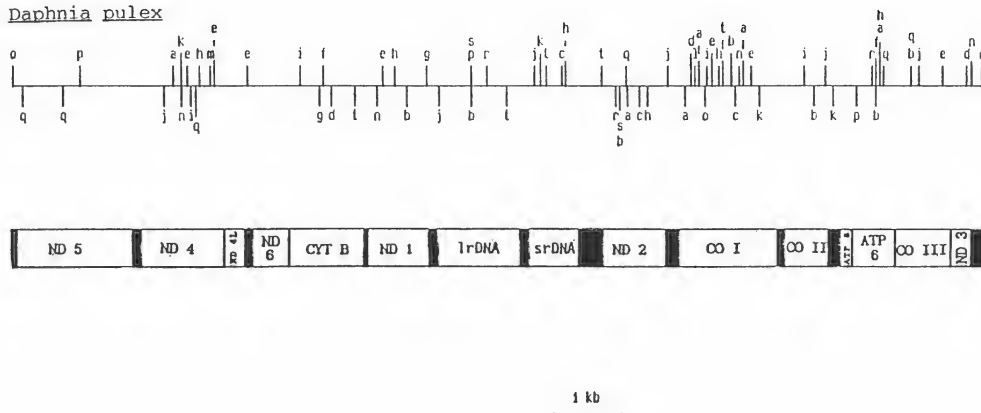


Figure 1. Restriction map of *Daphnia* mitochondrial DNA (modified from Crease *et al.* 1990). The letter codes are as follows: a=Apal; b=Aval; c=BamHI; d=BclI; e=BglII; f=BstEII; g=Clal; h=EcoRI; i=EcoRV; j=HindIII; k=HpaI; l=MluI; m=NcoI; n=PstI; o=PvuII; p=SstI; q=StuI; r=XbaI; s=XhoI; t=XmnI. Conserved sites within species are shown above the line.

precipitation, the fragments were resuspended in 10 μ l of water and combined to make a total of 20 μ l. The ligation was carried out by adding 10 μ l of ligation mix [20 μ l 10X ligation buffer (600 mM Tris, pH 7.5, 70 mM MgCl₂, 600 mM PEG, 10 mM DTT, 1 mM ATP) and 1 unit of T4 ligase]. This mixture was incubated overnight at 160 C. Ten μ l of this ligation mixture were added to 100 μ l of competent *E. coli* (XL-1 Blue), prepared by the method of Hanahan (1983). Following transformation, 10 μ l of the transformation mixture were plated on "blue" Luria-Bertani (LB) agar plates containing 0.5% IPTG, 40 μ g/ml X-gal, and 100 μ g/ml Ampicillin. The plates were incubated overnight at 37° C, and white colonies were picked according to Maniatis *et al.* (1982). Plasmids were screened for the appropriate inserts by isolation from transformed bacterial cells using the "mini-prep" procedure of Maniatis *et al.* (1982) and subsequent electrophoresis on 0.8% agarose gels.

DNA Sequencing

To prepare DNA of sequencing quality, 10 ml cultures of the desired clones were grown overnight in LB media and plasmid purified by the use of Promega Magic Mini-preps. Three micrograms of purified double-stranded DNA were alkaline-denatured using 0.2M NaOH at room temperature for 10 minutes. The mixture was neutralized by

the addition of 0.5 volumes 0.9M sodium acetate and the DNA was precipitated by the addition of three–four volumes of 100% ethanol. This pellet was washed with 70% ethanol and resuspended in 7 μ l of doubly distilled water. The DNA was sequenced using [³⁵SdATP] and T7 DNA polymerase with the Sequenase kit (United States Biochemical). All reactions were carried out according to manufacturer's directions. The M13-universal and M13 reverse primers were used in sequencing the ND4 and ND5 genes. All sequencing reactions were electrophoresed on 8% polyacrylamide gels, which were subsequently dried and exposed to autoradiographic film for 12–24 hours.

Sequence Analysis

The GCG group of programs for the VAX were used to align and translate sequence data. Consensus sequences were generated by determining the most frequent nucleotide for each site. The *Drosophila* genetic code (Clary and Wolstenholme 1985) was used to translate nucleotide sequences into amino acid sequences. Nucleotide diversity (average number of nucleotide differences per site) was estimated by equation 10.4 of Nei (1987) using 170 bp sequences for each gene that were present for all 11 individuals (one per population).

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      .       .       .       .
1  GCCCAATTTTCTAATCCTATCTTATTTTGATTAATACTGTTGGCGTTTCT 50
      |||  ||  ||  |||  ||  ||  ||  ||  ||  ||  ||  ||  ||
9034 TTTATGTTTAATTATGATTATTATATTTTGTATTATTATGTGCTTTTTT 8985

      .       .       .       .
51 AGTCAAGCTTCCCGTATATTTTGGACATTGTGACTTCCTAAGGCCGATG 100
      |||  ||  ||  |||  ||  |||  |||  |||  |||  ||  |||
8984 AGTGAAAATACCAATATTTTAGTACATTATGATTACCTAAAGCTCATG 8935

      .       .       .       .
101 TTGAGGCCCCAGTTGCAGGGTCTATAATTCTAGCGGGGTTTATTAAAG 150
      |||  |||  ||  ||  ||  |||  |||  |||  ||  |||  |||
8934 TTGAAGCTCCTGTATCTGGTTCTATAATTTTAGCTGGTATTATATTAATA 8885

      .       .       .       .
151 TTAGGGGGGTACGGAATAGTTCGAGTTGTCCTTACCGTCGAGTTAAGTC 200
      ||||  ||  ||  ||  ||  |||  ||  ||  ||  ||  ||
8884 TTAGGAGGTTATGGTTTATTACGAGTAATTAATTTTACAATTAATAAA 8835

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Figure 2. Alignment of *Daphnia* NADH dehydrogenase subunit 4 gene with *Drosophila yakuba*. *Daphnia* sequence is on top.

Results

Comparison of Nucleotide Sequences

The consensus sequences for ND4 and ND5 from the eleven individuals are aligned with *Drosophila yakuba* sequences in Figures 2 and 3 respectively. Overall, there were two mitochondrial types for ND4 and five different types for ND5 (Table 2). Summed over both loci, six different mitochondrial types are evident, indicating a high degree of sequence polymorphism. The sample frequency for all but one of these types is 2/11. The other type had a frequency of 1/11. There were two polymorphic nucleotide sites in ND4 (positions 33 and 40) and five in ND5 (positions 84, 89, 105, 123, and 210). The estimated nucleotide diversity (average number of nucleotide differences per site) was 0.22% for ND4 and 0.69% for ND5. The combined nucleotide diversity is estimated to be 0.51 %.

Both ND4 and ND5 showed divergence at the amino acid level. There were four amino acid substitutions among the eleven sequences at two different sites (position 30 in ND4 and position 89 in ND5). These two changes were tryptophan → cysteine in ND4 and isoleucine → threonine in ND5. The estimate of amino acid diversity (combined over both species for each locus) is 0.2%, about the same as the nucleotide diversity for ND4, but substantially less than the nucleotide divergence for ND5.

Contrary to the result from restriction endonuclease analyses (Crease *et al.* 1990), indi-

TABLE 2. Variable nucleotide sites for ND4 and ND5.

Individual	ND4 Position		ND5 Position				
	33	40	84	89	105	123	210
PA	A	C	T	C	C	C	T
TSP	A	C	T	C	C	C	T
BU	A	C	C	T	T	C	C
AM	A	C	C	T	T	C	C
FC19	C	T	T	T	C	C	T
FC23	C	T	T	T	C	C	T
17	A	C	T	T	T	C	C
ODL	A	C	C	T	T	T	C
LCU	A	C	C	T	T	T	C
HOS	A	C	T	T	C	C	T
KLA	A	C	T	T	C	C	T

viduals from the two *Daphnia* species do not form distinctive clades, as there are no fixed differences between the two species. The mtDNA genotypes between species are no more distant to each other than are genotypes within species.

Pattern of Substitution

Patterns of nucleotide substitution (Table 3) show that most of the substitutions among the eleven individuals were synonymous (i.e., did not result in an amino acid substitution) and occurred mainly at third base positions in codons. Combining all loci, there were eighteen synonymous substitutions

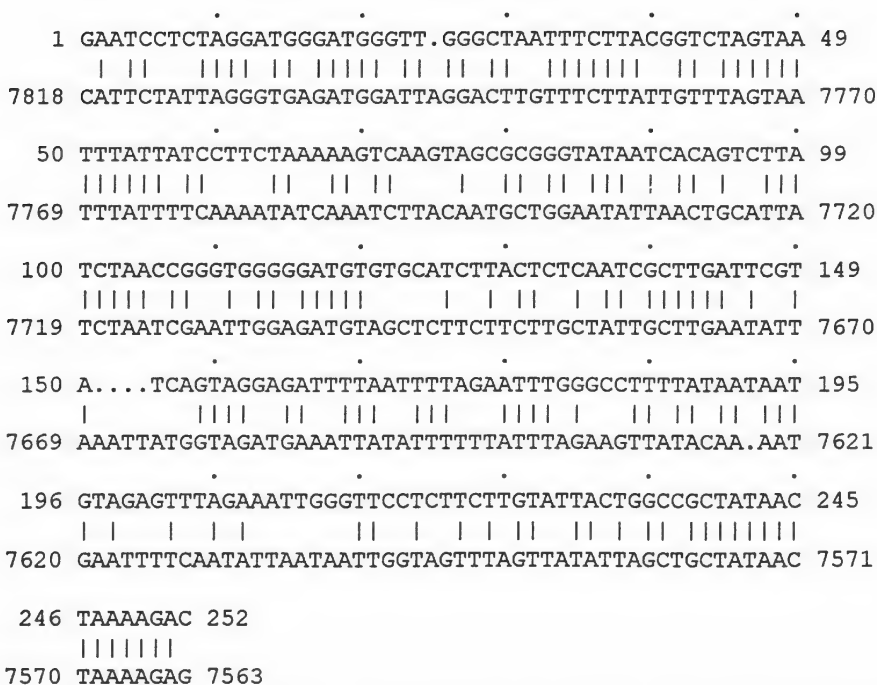


Figure 3. Alignment of *Daphnia* NADH dehydrogenase subunit 5 gene with *Drosophila yakuba*. *Daphnia* sequence is on top.

TABLE 3. Patterns of Nucleotide Substitution in *Daphnia*. Data are summed over all individuals.

Gene	bp	syn	non-syn	tsit	tvr
ND4	170	2	2	2	2
ND5	169	16	2	18	0
TOTAL	339	18	4	20	2

NOTE: bp = base pairs, syn = synonymous, non-syn = non-synonymous, tsit = transitions, tvr = transversions, ND4 = NADH sub-unit 4; ND5 = NADH sub-unit 5

and four non-synonymous substitutions distributed among the eleven individuals. There exists a strong transition bias in *Daphnia* mtDNA evolution measured both within and between species. The transition:transversion ratio for the two loci combined was 10:1.

Discussion

Estimates of diversity from restriction endonuclease (RE) data for *D. pulex* average about 0.006 (Crease

et al. 1990). Estimates of nucleotide diversity obtained from sequence data generally agree with those obtained from RE studies, but average slightly lower. Per locus estimates are very similar, but the total estimate is low due to little variability in ND4.

Sequence analysis of *Daphnia* mtDNA genes does not elucidate phylogenetic relationships among populations and species that are suggested for these populations at both the isozyme electrophoresis level (data not shown) and the mtDNA genome restriction level (Crease *et al.* 1990). A larger survey of sequence variability within the species would most likely reveal the patterns of phylogenetic structure that are evident in the larger restriction-site survey.

Amino-acid substitutions observed in this analysis occurred in both genes. In fact, estimates of amino-acid diversity for the ND4 gene are nearly as large as the estimates for nucleotide diversity. It has been suggested that the amino-acid replacement rate should approach the nucleotide substitution rate in genes that are less functionally constrained (Nei 1987). This has been the case

for other mtDNA genes from other organisms (*Drosophila*, Clary and Wolsteholme 1985; *Apis*, Pumo *et al.* 1992). The estimated degree of intraspecific variability at the amino acid level is shown to be on the same order as was predicted previously by molecular clock analyses (Lynch and Jarrell, 1993), despite the effects of recent bottlenecks (e.g., Pleistocene glaciations) on *Daphnia* populations.

When the equations 13 and 14 of Lynch and Jarrell (1993) are applied to estimated levels of amino acid divergence between *Daphnia* and *Drosophila*, estimates of the date of divergence of these two species are obtained (Table 4). The estimates for the two genes give similar estimated dates of divergence. When averaged over both loci, the data suggest that the *Daphnia-Drosophila* split may have occurred about 320 million years ago. Fossil *Daphnia*-like animals are known from the Permian (280 million years ago; Smirnov 1970), so this may be a relatively accurate estimate.

TABLE 4. Amino Acid Divergence, Δ , and Estimated Time to Common Ancestor (MY) with 95% confidence limits between *Daphnia* and *Drosophila*.

	ND4	ND5
Δ	0.283	0.370
MY +/- CL	300 +/- 109	340 +/- 188

If all nucleotide substitutions are equally likely to occur, then transversions should outnumber transitions by two to one over evolutionary time. This is clearly not the pattern observed. Data from a variety of taxa and for a variety of genes indicate that there is in fact a transition bias. Data from *Daphnia* mitochondrial DNA confirm this bias as well. For *Daphnia*, there were nearly ten transitions for each transversion. Although this is less than the bias that is observed for many vertebrates, it is still substantially different from the neutral prediction. Thus, it is possible that this transition bias is a fairly widespread phenomenon.

The cause of the bias is unknown. One hypothesis is that variations away from the neutral expectation are caused by activation during DNA replication of mutator genes that favor transitions (Jukes 1987). Such mutator genes are known to exist in bacterial (Cox and Yanofsky 1967) and viral (Speyer 1965) systems, but their existence in eucaryotic systems is hypothetical.

DeSalle *et al.* (1987) suggested that the cause of the bias is due to inefficient repair systems of mitochondria. There is evidence for lower levels of repair for mitochondria (Clayton 1984, 1991), and bacterial mutants deficient in repair show mutational spectra that are very similar to that of mtDNA (Schaaper and Dunn 1987). However, recent research with γ -DNA polymerase, the only known eucaryotic DNA polymerase to be found in mitochondria, suggests that it may possess 3' to 5' exonuclease activity and proof-reading capabilities (Kunkel and Musbaugh 1989). Moreover, certain types of repair enzymes have been identified in mitochondrial fractions (Tomkinson *et al.* 1990), although their use still remains questionable.

In light of the genetic code, transversions should not outnumber transitions by a factor of two. In protein-coding DNA, the majority of synonymous changes within two-fold and six-fold degenerate codon groups are transitions. Among two-codon groups, transversions in the third position of the codon result in an amino acid change, whereas a transition at the third position specifies the same amino acid. The same pattern is observed in the first position of the triplet code in six codon groups. Thus, it seems likely that transitions are selectively favorable to transversions and should occur more frequently during the replicative process. The observations that transitions are the most likely mispair during replication (Topol and Fresco 1976) and that the bias is fairly widespread among different taxa and loci, support the contention that selection has shaped the replicative machinery to be more tolerant of transitional changes during replication. Thus, it is unnecessary to invoke any special properties of mitochondria to explain a transition bias.

Expanding on the rationale of Jukes (1987), the neutral prediction of nucleotide substitution should not be for a transversion bias if the majority of substitutions are likely to be synonymous (as is the case for mtDNA which is under strong functional constraint (Jukes and Bhushan 1986)). Using the human mtDNA genetic code, 62 of the potential 126 synonymous substitutions are transitions, suggesting a neutral ratio of nearly one transition to each transversion (due to the difference in genetic code, there exists a slight expected transversion bias, 1.25:1 for nuclear DNA). Deviations away from this neutral prediction would most likely reflect the amino acid composition and codon usage bias of proteins.

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Literature Cited

- Avise, J. C., J. Arnold, R. M. Ball, E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reeb, and N. Saunders. 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Ann. Rev. Ecol. Syst.* 18:489-522.
- Beckenbach, A. T., Y. W. Wei, and H. Liu. 1993. Relationships in the *Drosophila obscura* species group, inferred from mitochondrial cytochrome oxidase II sequences. *Mol. Biol. Evol.* 10:619-634.
- Bessho, Y., T. Ohama, and S. Osawa. 1992. Planarian mitochondria I. Heterogeneity of cytochrome c oxidase subunit I gene sequences in the freshwater planarian, *Dugesia japonica*. *J. Mol. Evol.* 34:324-330.
- Brown, G. G. and M. V. Simpson. 1982. Novel features of animal mtDNA evolution as shown by sequences of two rat cytochrome oxidase subunit II genes. *Proc. Natl. Acad. Sci. USA* 79:3246-3250.
- Brown, W. M., M. George, Jr., and A. C. Wilson. 1979. Rapid evolution of animal mitochondrial DNA. *Proc. Natl. Acad. Sci. USA* 76: 1967-1971.
- Brown, W. M., E. M. Prager, A. Wang, and A. C. Wilson. 1982. Mitochondrial DNA sequences in primates: tempo and mode of evolution. *J. Mol. Evol.* 18:225-239.
- Clary, D. O. and D. R. Wolstenholme. 1985. The mitochondrial DNA molecule of *Drosophila yakuba*: nucleotide sequence, gene organization, and genetic code. *J. Mol. Evol.* 22: 252-271.
- . 1987. *Drosophila* mitochondrial DNA: conserved sequences in the A+T-rich region and supporting evidence for a secondary structure model of the small ribosomal RNA. *J. Mol. Evol.* 25:116-125.
- Clayton, D. A. 1984. Transcription of the mammalian mitochondrial genome. *Ann. Rev. Biochem.* 53:573-594.
- . 1991. Replication and transcription of vertebrate mitochondrial DNA. *Ann. Rev. Cell Biol.* 7:453-478.
- Cox, E. C. and C. Yanofsky. 1967. Altered base ratios in the DNA of an *Escherichia coli* mutator strain. *Proc. Natl. Acad. Sci. USA* 58:1895-1902.
- Crease, T. J., D. J. Stanton, and P. D. N. Hebert. 1989. Hierarchical analysis of population genetic variation in mitochondrial and nuclear genes of *Daphnia pulex*. *Mol. Biol. Evol.* 7:444-458.
- Crease, T. J., D. J. Stanton, and P. D. N. Hebert. 1989. Polyphyletic origins of asexuality in *Daphnia pulex*. II. Mitochondrial DNA variation. *Evolution* 43: 1016-1026.
- De Salle, R., T. Freedman, E. M. Prager, and A. Wilson. 1987. Tempo and mode of sequence evolution in mitochondrial DNA of Hawaiian *Drosophila*. *J. Mol. Evol.* 26:157-164.
- Edwards, S. V. and A. C. Wilson. 1990. Phylogenetically informative length polymorphisms and sequence variability in mitochondrial DNA of Australian song-birds (*Pomatostomus*). *Genetics* 126:695-711.
- Giorgi, C., F. DeLuca, and c. Saccone. 1991. Mitochondrial DNA in the sea urchin *Arbacia lixula*: nucleotide sequence differences between two polymorphic molecules indicate asymmetry of mutations. *Gene* 103:249-252.
- Hanahan, D. 1983. Studies on transformation of *Escherichia coli* with plasmids. *J. Mol. Biol.* 166: 557-580.
- Hillis, D. M., A. Larson, S. K. Davis, and E. A. Zimmer. 1991. Nucleic acids III: sequencing. In: *Molecular Systematics*, D. M. Hillis and C. Moritz (eds). Sinauer Press, MA.
- Jukes, T. H. 1987. Transitions, transversions, and the molecular evolutionary clock. *J. Mol. Evol.* 26:87-98.
- Jukes, T. H. and V. Bhushan. 1986. Silent nucleotide substitutions and G+C content of some mitochondrial and bacterial genes. *J. Mol. Evol.* 24:39-44.
- Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Paabo, F. X. Villablanca, and A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc. Natl. Acad. Sci. USA* 86: 6196-6200.
- Kunkel, T. A. and D. W. Musbaugh. 1989. Exonucleolytic proofreading by a mammalian DNA polymerase β . *Biochemistry* 28:988-995.
- Lynch, M. 1983. Ecological genetics of *Daphnia pulex*. *Evolution* 37: 358-374.
- Lynch, M. and P. E. Jarrell. 1993. A method for calibrating molecular clocks and its application to animal mitochondrial DNA. *Genetics* 135: 1197-1208.
- Maniatis, T., E. F. Fritsch, and J. Sambrook. 1982. *Molecular Cloning: A Laboratory Manual*, Cold Spring Harbor Publications, Cold Spring Harbor.
- Moritz, C., T. E. Dowling, and W. M. Brown. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Ann. Rev. Ecol. Syst.* 18:269-292.
- Nei, M. 1987. *Molecular Evolutionary Genetics*. Columbia University Press, MA.
- Pumo, D. E., C. J. Phillips, M. Barcia, and C. Millan. 1992. Three patterns of mitochondrial DNA nucleotide divergence in the meadow vole, *Microtus pennsylvanicus*. *J. Mol. Evol.* 34:163-174.
- Sanger, F., S. Nicklen, and A. R. Coulson. 1977. DNA sequencing with chain-terminating inhibitors. *Proc. Natl. Acad. Sci. USA* 74:5463-5467.
- Schaaper, R. M. and R. L. Dunn. 1987. Spectra of spontaneous mutations in *Escherichia coli* strains defective in mismatch correction: the nature of *in vivo* DNA replication errors. *Proc. Natl. Acad. Sci. USA* 84: 6220-6224.
- Smirnov, N. N. 1970. Cladocera (Crustacea) iz permskikh otlozheniy Vostochnogo Kazakhstana. *Paleontol. Zh.* 3: 95-100.
- Speyer, J. 1965. Mutagenic DNA polymerase. *Biochem. Biophys. Res. Comm.* 21:6-10.
- Stanton, D., T. J. Crease, and P. D. N. Hebert. 1991. Cloning and characterization of *Daphnia* mitochondrial DNA. *J. Mol. Evol.* 33:152-155.

- Thomas, W. K. and A. T. Beckenbach. 1989. Variation in Salmonid mitochondrial DNA: evolutionary constraints and mechanisms of substitution. *J. Mol. Evol.* 29:233-245.
- Thomas, W. K. and A. C. Wilson. 1991. Mode and tempo of molecular evolution in the nematode *Caenorhabditis*: cytochrome oxidase II and calmodulin sequences. *Genetics* 128:269-279.
- Tomkinson, A. E., R. T. Bonk, J. Kim, N. Bartfield, and S. Linn. 1990. Mammalian mitochondrial endonuclease activities for ultraviolet-irradiated DNA. *Nucleic Acids Res.* 18:929-935.
- Topol, M. D. and J. R. Fresco. 1976. Complementary base pairing and the origin of substitution mutations. *Nature* 263:285-289.
- Wayne, R. K., A. Meyer, N. Lehman, B. Van Valkenburgh, P. W. Kat, T. K. Fuller, D. Girman, and S. J. Obrien. 1991. Large sequence divergence among mitochondrial DNA genotypes within populations of eastern black-backed jackals. *Proc. Natl. Acad. Sci. USA* 87: 1772-1776.

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Robert T. Lackey,¹ Environmental Research Laboratory, United States Environmental Protection Agency, 200 SW 35th Street, Corvallis, Oregon 97333

The Future of Ecological Risk Assessment²

Abstract

Risk assessment has become a popular tool to help solve ecological problems. The basic concept is not new and has been applied to diverse decision problems. The application to ecological problems, especially complex ecological problems, is fairly recent and controversial. The fundamental and most important elements of the controversy revolve around two key points: (1) a person's implicit "worldview;" and (2) the assumption of who (or what) receives the benefits and who (or what) pays the costs for ecological "decisions." A person's attitude toward risk assessment is, at least implicitly, defined by a worldview. It is the worldview which defines how each of us react to risk assessment applied to ecological problems. How the question of benefits and costs is defined also defines the appropriate use, if any, of ecological risk assessment. The future of ecological risk assessment will almost certainly follow the course of other analytical tools—enthusiastic support, rapid, widespread adoption and use, then disillusionment and rapid replacement with newer approaches, but with continued use for a greatly constrained set of ecological issues.

Introduction

There are many opinions about the philosophical and moral basis for ecological risk assessment, how risk assessment is used, how it is abused, and what a better alternative might be. The definition of ecological risk assessment ("the process that evaluates the likelihood that adverse ecological effects are occurring, or may occur, as a result of exposure to one or more stressors") seems simple enough,

but an entire symposium has been devoted to evaluating the philosophical basis for ecological risk assessment and what alternatives might be appropriate. No consensus emerged and it was one of the most intellectually and emotionally divisive meetings I have ever attended. The interesting question to me is: why is this issue so divisive?

An analysis of the debate over ecological risk assessment shows that some individuals have dramatically different positions and share little in common, but others accept the same basic philosophical tenets and differ on relatively minor points (Lackey, 1994; 1995). Some individuals pitch the classical risk paradigm of commerce, industry, and insurance adapted for ecological problems with little modification, while others challenge the very foundation and morality of the commonly used approach. Many individuals offer modifications, or caution us about the circumstances for

¹Dr. Lackey is Deputy Director of EPA's Environmental Research Laboratory. He is also Professor of Fisheries at Oregon State University and Associate Director of the Center for Analysis of Environmental Change.

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using risk assessment. A few offer alternatives. It is not my purpose to advocate any particular view, but rather to try to understand the nature of the debate.

It is easy to sink into the mire of detail of how to conduct ecological risk assessments or the advantages and disadvantages of various analytic tools. The ecological risk literature is dominated by a preoccupation with technique and practice. The important debate, however, revolves around two key points: (1) a person's implicit "worldview"; and (2) the assumption of who (or what) receives the benefits and who (or what) pays the costs for ecological "decisions."

A Proposed Worldview

We all look at risk assessment implicitly using a *five dimensional worldview*. Our reaction to ecological risk assessment as a concept and tool is probably also defined by one's collective positions on *each* of these five elements. Much of the debate over risk assessment may be couched in arguments over the details of *how* to do a risk assessment, but the debate is fundamentally over differences in elements of the worldview.

The *first* and most important dimension to a worldview is our perception of the condition of our *transport*. Recognized or not, we are *all* on a journey through our lives and the lives of our ancestors and progeny. As individuals and as a society, *what is the ecological condition of our transport?* Are we passengers on the *Titanic*—or are we aboard the *Loveboat*? The *Titanic* view is that we are in deep trouble on ecological issues. Something needs to be done *now* or the planet is going down the tube. Biological diversity is disappearing at a crisis rate; human population growth is the number one problem; the icebergs are there, they are formidable and unforgiving, and the consequences are obvious and catastrophic. From the *Titanic* perspective, risk assessment is nothing more than the government rearranging deck chairs while telling passengers: "Trust me. I'm from the government and things are under control."

But others take what might be best called the *Loveboat* view. Yes, there are some choices we have to make concerning ecological issues, but there are also choices about economic well being, individual freedom, and the aspirations of economically less well off individuals and groups. Within limits, however uncertain these limits might be, we

can use the natural world for the betterment of us all. Our financial resources and energies are limited and we ought to balance the needs of the natural environment against other needs of society. Compromise is the order of the day and works best in a democracy—after all is said and done. From the *Loveboat* perspective, risk assessment is a reasonable attempt to bring rationality to solving important public choice questions, but we don't have an ecological crisis that existing institutions cannot handle.

The *second* dimension of our worldview is the *confession*. We have all read or heard the results of risk assessments, but are they to be believed and trusted? *These* are the confessions. Specifically, are risk assessments *in practice* accurate, unbiased, impartial analyses, or are they so tainted with hidden assumptions and valuebased decisions that they are virtually worthless in public policy debates and might even be misleading? If they are misleading, is it intentional? If it is intentional, what agenda is being advanced?

Now I call this element of our worldview the issue of the *confession* because it is well known that with sufficient torture, a prisoner will confess to any transgression. Only the creativity of the torturer limits the range of possible confessions. Such has been said about benefit/cost analysis, ecological modeling, environmental impact analysis, and—yes—even risk assessment. The risk assessment "problem" can be defined in such narrow terms as to make the analysis technically feasible, but the results are misleading to the real policy debate. Few go as far as alleging that scientists and analysts are tortured to provide the *right* answers, but the role of funding, career rewards, and prestige can be every bit as effective in the hands of skillful individuals and organizations as is torture for a creative and committed prison guard. For those individuals who do not trust the *process* of conducting risk assessments, the *results* (the confessions) will be equally untrustworthy. Some participants in the debate appear to be concerned about the nature of the confession; others are not.

The *third* dimension of one's worldview is the *gospel*—some speakers have followed the gospel of *enlightenment* and some followed the gospel of *rationality*.

The gospel of *enlightenment* is defined by a moral code, a set of religious beliefs, some ethical tenets from deep ecology, new age religion, Rush Limbaugh, or from any other source. The point is

that there is a truth. Some argue that this view is the antithesis of the scientific enterprise. Others allege that some scientists (particularly "ecologists") wear the cloak of the scientist, but actually practice enlightenment of a religious "environmentalism."

Others follow the gospel of *rationality*—society has to balance competing alternatives, and risk assessment helps do this. Closely tied to the gospel of rationality is the mantra of *win-win*. Such a secular icon as *win-win* is intrinsically appealing to rationalists. While the gospel of *enlightenment* is highly skeptical of ecological risk assessment, ecological risk assessment is so logical and obvious, according to the gospel of *rationality*, that it must be difficult for these adherents to even see the dichotomy.

The *fourth* dimension of one's worldview is the *schedule*. A fact of life is that trains need to run on time. Governments have collapsed because they could not deliver on this simple requirement. The public expects government, at a minimum, to execute housekeeping tasks effectively and efficiently. Democracy is often perceived to be—and it may well be—inversely proportional to efficiency. Regulating the use of chemicals, protecting ecological resources, preserving biological diversity, for example, are legitimate tasks of government and we ought to have *professionals* accomplish these tasks in the most efficient manner possible. A government that cannot accomplish these things, or keep the trains running on time, is a failure. Let the professionals handle these things!

Or, alternatively, is it really that important to keep the trains running on time? Perhaps we ought to ask: what really happens if the schedule slips? What happens if the trains run only when they are full? Where are the trains going? Do we even need trains? Are people better off with or without trains and their cursed schedules? Governments and bureaucracies will tend to see the problem as one of how to make them run on time; society *might* be best served if we looked at the alternatives to mobility. In short, it is how the ecological *problem* is formulated in ecological risk assessment that is most critical to society. How the problem is formulated will largely define the answer.

The *fifth* dimension of our probable worldview might best be described as the *water glass* phenomenon. A glass with a water level midway is half full—and half empty. How the level is viewed

totally depends on the viewer. The concept of *risk* for ecological issues is also entirely defined by the viewer. Risk is singularly a human construct. One person's risk may well be another's benefit. For example, wild horses in North America may be regarded as either a benefit, a noble treasure of the west, or as a risk, a biological pest that ought to be eradicated to protect "native" fauna and flora.

Part of the difficulty with applying *risk* assessment is that, by definition, risk is *adverse*. In ecological systems there is no "good" nor any "bad," and certainly nothing "adverse." In contrast, an ecological "change" is labeled "adverse" by individuals, organizations, or societies. The only way to convert an ecological characteristic to adverse is to make a value judgment. To conduct a risk assessment means that *someone* made a value judgment of which ecological condition will be defined as *adverse*. Who makes such choices: the professional elite? those in power? the general public? elected officials? Are scientists and their fellow travelers being used as tools in what is essentially a debate over values? Or, are scientists using the process of risk assessment to impart *their* values? Most participants in the debate over the appropriateness of ecological risk assessment skillfully evade this issue—or raise it ever so tactfully.

Benefits and Costs

Apart from one's worldview, how one answers the question of benefits and costs defines the appropriate role, if any, of ecological risk assessment. More specifically, the question is: "who receives benefits and who pays the costs?" Two views of the world compete.

The first, most comfortable to most of us and the most amenable to scientific information, is the *anthropocentric* view of the earth and its resources. The assumption is that all benefits from decisions affecting ecological systems are accruable to humans. To be sure, we may preserve wilderness that few actually visit, protect from extinction obscure species that have no tangible value, and spend vast sums to restore habitats for species of very limited market value. All these efforts still provide benefits to people; the benefits may be nonmarket, non-monetary, and merely a way to "buy" some indeterminate form of future insurance, but they all benefit man. Nature may benefit, but only as a byproduct of the primary decision. The entire regulatory framework to protect ecosystems is set up, at least

implicitly, under this assumption. We protect biodiversity because some people believe bad things may happen to future generations if we do not. We preserve wilderness areas because just knowing that unaltered ecosystems exist has value to people.

The alternate world view is ecocentered, often called *earthcentered*. This is the realm of deep ecology and certain religious or philosophical creeds. The basic tenet is that benefits accrue to all species; humans are only one species and are no more important than the others. It follows, then, that all species must be treated equally. We protect ecosystems because all animals and plants have a right to exist. The importance of biodiversity is because it is morally right, not because biodiversity is or might be important to man. From an anthropocentric perspective, risk assessment weighs ecological alternatives from the value to man.

Risk assessment, at least as currently formulated, is an anathema to those holding the earth-centered view. The mere discussion of ranking risks to ecosystems would be similar to deciding which humans should live or die. The intensity of the debate about the morality of abortion is similar philosophically. The debate is morally based; rational argument plays little or no role. For example, from this philosophy come uncomfortable questions such as: "Should we be subjecting thousands of animals to suffering so the fragrances of

our shampoos do not sting our eyes?" It is easy to dismiss this view in a room full of rationalists, but the ecocentric view is becoming increasingly important in the political process. For those individuals who hold an ecocentric worldview, or those who lean in this direction, risk assessment will not be well received. From an ecocentric perspective, risk assessment will likely be perceived as a form of ecological triage.

Conclusion

What, then, is the future of ecological risk assessment? Of course, there is no definitive answer, but whatever the future is for ecological risk assessment, it will depend in large part on the emerging consensus on the five elements of a worldview and in the answer to the fundamental question of who (or what) receives benefits and who (or what) pays costs (anthropocentric vs. ecocentric).

If the past is a guide, the future of ecological risk assessment will follow the course of other tools such as bioassays, environmental impact assessments, modeling, expert systems, geographic information analysis, total quality management, and adaptive management—initial enthusiastic support, rapid, widespread adoption and use, then disillusionment and rapid replacement by newer approaches, but with continued use for a greatly constrained set of ecological issues.

Literature Cited

- Lackey, Robert T. 1994. Ecological risk assessment. *Fisheries*, Bulletin of the American Fisheries Society. 19(9): 14-18.
- Lackey, Robert T. [1995 In Press]. Is ecological risk assessment useful for resolving complex ecological problems? IN Stouder, Deanna J., Peter A. Bisson, and Robert J. Naiman (editors). *Pacific salmon and their ecosystems: status and future options*. Chapman and Hall, Publishers, N.Y.

Summary of Minutes of the Board Meeting of the Northwest Scientific Association

(Idaho Falls, Washington; March 8, 1995)

Submitted by Denis Lavender, Secretary

1. David Hansen reported that Association membership has remained level over the past year. It appears that the current dues structure is adequate for the Association's needs.
2. David Peterson reported that there will be a new cover design for *Northwest Science* starting in 1995, as well as a new Forum section that will feature short articles and letters.
3. A new brochure is now being used to solicit donations to the Association's research fund. This was helpful in procuring a donation of \$3000 from the Idaho Falls Chamber of Commerce for the 1995 Association meeting.
4. The discipline Computer Science has now been added to those which currently appear on Association letterhead.
5. Michael Pitt will remain chair of the Honors and Awards Committee. Jerry Wolff is new chair of the Student Awards Committee. Mark Sheehan is new chair of the Nominating Committee. A new Long Range Planning Committee was formed to assess long-term goals for the Association and development of greater support for the research fund; members include Jan Henderson, Barry Keller, Kenneth Hammond, David Hansen, and Denis Lavender.
6. Planning is underway for the 1996 annual meeting at Pacific Lutheran University, Tacoma, Washington, March 21-24. The 1997 annual meeting, originally scheduled for the third week of March at Eastern Washington University, Cheney, Washington, may be held in Spokane, Washington instead. Negotiations are underway to hold the 1998 meeting at The Evergreen State University, Olympia, Washington.



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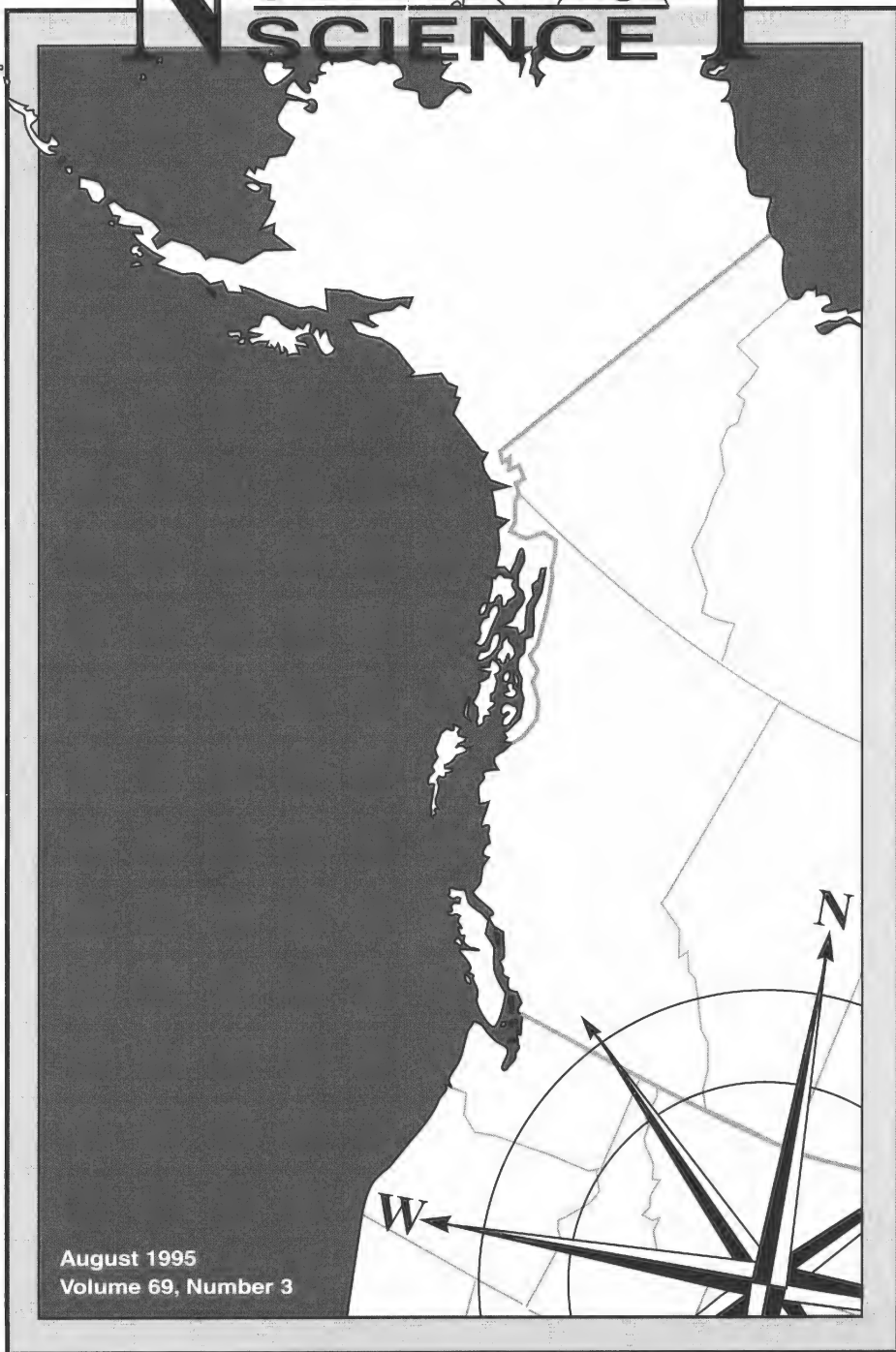
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at

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The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for \$20 per year (\$10 per year for students). Institutional memberships, \$40 per year. Sustaining membership, \$35 per year for individuals and \$100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

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Editor of *Northwest Science*

David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, Box 352100
Seattle, Washington 98195
Telephone: 206-543-1587
Fax: 206-685-0790
Internet: wild@u.washington.edu

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L. D. Daniels, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

P. L. Marshall, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

R. E. Carter, TimberWest Forest Ltd., P.O. Box 10017, 700 West Georgia Street, Vancouver, British Columbia, Canada V7Y 1A1

and

K. Klinka, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

Age Structure of *Thuja plicata* in the Tree Layer of Old-Growth Stands near Vancouver, British Columbia

Abstract

Age and diameter data were collected from 720 sound stumps (diameter ≥ 7.5 cm) of *Thuja plicata* (western redcedar) trees from 15 old-growth submontane cutover sites, within three watersheds near Vancouver, B.C. The relationship between age and dbh was quantified by regression analysis. The age structure on different sites was compared using age frequency distributions.

Regression models revealed weak, but still significant, relationships between age and diameter at breast height. Age distribution curves showed that the *Thuja* stands had been uneven-aged. The predominance of peak age classes indicated that establishment had been episodic and the populations were not in demographic equilibrium. We hypothesize that wind and fire disturbances and long-term climatic variation influenced the population dynamics and can explain the peaks observed in the age structures. Within the study area, *Thuja* populations are probably in a continual state of disequilibrium.

Introduction

Thuja plicata Donn ex D. Don (western redcedar) is a valuable species with commercial importance and ecological and aesthetic values. To manage the species requires knowledge of its population dynamics and the processes affecting regeneration and growth. Evaluation of stand structure yields information about regeneration and development (Lorimer 1985), but its value in understanding the dynamics of *Thuja* remains under-used (Oliver et al. 1988). Past studies have often been limited to interpreting diameter distributions (Schmidt 1955, Gregory 1957, Franklin and DeBell 1988, Keenan 1993), since age determination is difficult because of large size and frequent heartwood decay. Size can be used to interpret the population dynamics, but only when the relationship between tree age and size is strong (Lorimer 1985). Moreover, the age-size relationship has been shown to vary with site for some species, complicating interpretation of their dynamics (Veblen 1986, Stewart 1986). Of the studies cited, only Keenan (1993) reported the relationship between tree age and size. The value of diameter distributions for evaluating the dynamics of *Thuja* have yet to be critically assessed.

In this exploratory study, we provide the first replicated age analysis of *Thuja* in old-growth submontane forests of coastal British Columbia. Tree ages were determined from field counts of sound stumps from recently cut stands. We found the relationship between age and diameter at breast height (dbh) to be highly variable, making dbh a poor predictor of tree age. We derived age class distributions for 15 sites from which we generated three hypotheses regarding *Thuja* population dynamics and disturbance.

Methods

Study Sites

The study was conducted in the Capilano, Coquitlam, and Seymour watersheds, collectively 57,791 ha, located north of Vancouver, British Columbia. The study sites were in the Very Wet Maritime Coastal Western Hemlock biogeoclimatic subzone, within the perhumid, cool mesothermal climatic type (Klinka et al. 1991). Soils were steep-slope, coarse-skeletal, Ferro-Humic Podzols (Agriculture Canada Expert Committee on Soil Survey 1987) derived from colluvium and glacial till, and underlain by granitic rocks.

Fifteen study sites (A to O), five in each watershed, were selected for study. Each was a cutover area between 4 and 13 ha (Table 1). The sites were various aspects at elevations from 400 to 825 m, but all were on midslopes and had fresh to moist soil moisture regimes and medium soil nutrient regimes (Klinka et al. 1989). The stands had been cut since 1986, but were not slash burned. According to forest inventory, each had been dominated by *Thuja* >250 years old, but contained mature *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and *Abies amabilis* Dougl. ex Forbes (Pacific silver fir). *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) had been present in four of the stands (E, J, M, and N). We considered these sites representative of *Thuja*-dominated stands in the three watersheds, because the cutovers were continuous with extant stands typical of the submontane forest.

Sampling Methods

We sampled both sound and decayed stumps at each study site. Decayed stumps had partially rotten heartwood, but had been alive when the stand was cut. The decayed stumps were measured to test the assumption that specific size classes were not missed in our analysis of sound stumps alone. Age counts on sound stumps ensured that full ages of trees were determined.

Two sampling designs were used: the first on four sites (A, C, D, and E); the other on the remaining sites. For the first design, two parallel lines on each study site divided the cutover area into three equal portions. Six sampling points were uniformly distributed along each line. The four sound *Thuja* stumps closest to each point were sampled, for a total of 48. At each of three randomly selected points, decayed stumps were

TABLE 1. Site descriptions and age summaries for *Thuja plicata* in the tree layer on 15 study sites (for each site, n = 48) and for sites stratified by location and aspect (for each location and aspect, n = 240)

Site	Aspect	Elev. (m)	Area (ha)	Age (years)					
				Mean	S.D.	Median	Min.	Max.	Range
Capilano									
A	NW	620	6.0	395	164	421	114	826	712
B	NE	580	10.8	305	150	291	95	727	632
C	N	550	9.7	504	174	491	160	1051	891
D	SW	790	6.1	294	153	256	93	757	664
E	S	600	12.5	316	184	263	75	915	840
Seymour									
F	E	500	6.0	451	196	436	101	985	884
G	N	425	6.7	369	145	351	120	678	558
H	W	825	8.4	356	165	346	128	768	640
I	E	800	6.1	295	145	284	93	875	782
J	SE	520	6.4	479	157	462	206	792	586
Coquitlam									
K	NW	500	9.7	421	181	374	139	814	675
L	W	400	4.3	318	138	273	150	670	520
M	S	700	12.1	424	120	432	146	806	660
N	SE	500	12.8	311	116	309	126	695	569
O	E	450	5.8	346	109	331	78	535	457
Location									
Capilano watershed				363	182	357	75	1051	976
Seymour watershed				390	175	367	93	985	892
Coquitlam watershed				364	143	339	78	814	736
Aspect									
North				399	175	405	95	1051	956
East/West				353	161	331	78	985	907
South				365	164	351	75	915	840

sampled within a circular plot with a radius equal to the distance to the outermost sound stump. A mean of 17.8 decayed stumps (S.D. = 11.45) were measured within each plot but this design was time-consuming. It was replaced with the second design, in which we located all sound *Thuja* stumps within each study site, from which 48 were randomly selected from the entire cutover area for measurement. From the 48 sound stumps, two stumps were randomly selected around which circular plots of 12 m radius were established. All decayed stumps within each circular plot were sampled.

Sampling was restricted to the tree layer, since the study was conducted on cutover areas. Stumps with a diameter ≥ 7.5 cm were assumed to be part of the tree layer, normally defined as trees of height ≥ 10 m (Luttmerding et al. 1990). At all stumps, we measured the diameter including the bark (cm) and the uphill and downhill vertical distances (cm) from the upper surface of the stump to the ground, to calculate mean stump height. Field counts of the annual rings on sound stumps determined the ages. For weathered stumps or those with poorly distinguishable rings, a V-gouge was cut into the stump to expose a fresh surface and a 10X hand lens was used to count the rings.

Data Analysis

We calculated dbh from mean stump height and diameter measurements using conversion tables (Demaerschalk and Omule 1978). The dbh of decayed stumps were evenly distributed and ranged from 18 cm to 312 cm, indicating that decay was not dependent on tree size. We did not miss trees of specific sizes by considering only sound stumps. Given the broad range in size of decayed stumps, we assumed no age cohorts were missed and the

survey of sound stumps alone was an unbiased representation of the structure of *Thuja* in the original stands. Further analyses were conducted on data from sound stumps.

Age at stump height was corrected to total age (in 1991) by using the age of seedlings from the understory of extant stands nearby (Daniels 1994). Stumps were grouped into 50 cm height classes, then we added the mean seedling age for each height class to the stump age count to give the total tree age (Table 2).

To quantify the relationship between age and dbh we derived site-specific regression equations and a general equation, for all sites combined. Both age and dbh were logarithmically transformed to provide a function describing the relationship between age and size of *Thuja* trees ($\log_{10}[\text{age}] = b_0 + b_1 \times \log_{10}[\text{dbh}]$) which met the assumptions of regression analysis (Zar 1984). The standard error of the estimate (SEE) for each transformed model was back-transformed to present its variation in original units (years). For all statistical tests, significance was set at $\alpha = 0.05$.

Age frequency distributions (50-year classes) were prepared for each study site and for all data combined. All trees ≥ 900 years old were included in a single class. The mean class frequency and its standard deviation was calculated for each distribution. We defined “peak” age classes as those with class frequencies greater than the mean frequency plus one standard deviation, and compared the occurrence of peaks among sites.

Results

The ages of sound stumps ≥ 7.5 cm dbh ranged from 75 to 1051 years; mean ages for sites ranged from 294 to 504 years; and median ages from

TABLE 2. *Thuja plicata* seedling ages by height class. To calculate total age of trees, the mean seedling age corresponding to stump height was added to the field count of stump age.

Height (cm)	No. of stumps	No. of seedlings	Seedling ages (years)			
			Mean	S.D.	Minimum	Maximum
≤50	142	119	17	6.76	5	45
51 - 100	361	71	25	8.78	11	48
101 - 150	172	16	31	10.73	16	52
151 - 200	37	5	33	8.56	23	42
201 - 250	8	4	44	15.97	24	62

256 to 491 years. The mean ages within Capilano, Seymour, and Coquitlam watersheds were 363, 390, and 364 years, respectively. Means for north, east/west, and south aspects were 399, 353, and 365 years, respectively (Table 1).

The range and standard deviation of mean ages for all study sites were high (Table 1). The variability in ages was also reflected in the age-size regression models. Although these models indicated that size explains a statistically significant proportion of the variation in age, the relationships were weak. The R^2 values of age on dbh ranged from 0.32 to 0.79 and the corresponding SEE's ranged from 67 to 137 years for the site-specific models. The general regression equation was statistically significant ($R^2 = 0.65$, $p \leq 0.001$); however, its SEE of age on dbh of 109 years was high (Figure 1).

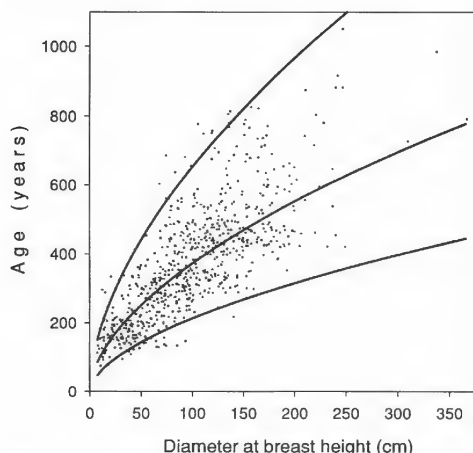


Figure 1. Relationship between age and dbh for *Thuja plicata*. The middle curve marks the regression line [$\log_{10}(\text{age}) = 1.435 + 0.568 \log_{10}(\text{dbh})$]. Upper and lower curves mark the regression line ± 1.96 SEE, including 95% of observations ($n = 720$).

The age class distributions showed the *Thuja* in the tree layer were uneven-aged with ranges from 457 to 891 years on each site. The age class distribution for all *Thuja* trees combined showed the highest class frequencies between 150 and 500 years. Peak classes were the 200 (200 = upper limit of class from 151 to 200 years), 350, 450, and 500 year classes (Figure 2). Examination of age class distributions by study site (Figure 3) showed five sites (A, D, E, H, and L) to have had

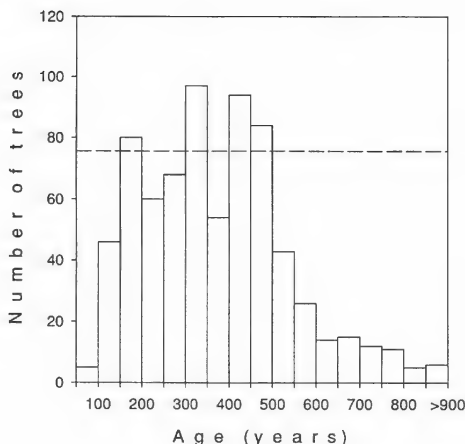


Figure 2. Age frequency distributions of 720 *Thuja plicata* in the tree layer on 15 study sites. The x-axis shows the upper limits of 50 year classes. The broken line marks the mean class frequency + 1 standard deviation of the mean; classes with frequencies above this line are "peak" classes.

peaks in the 200 year class; eight sites (D, F, G, H, I, K, N, and O) to have had peaks in the 350 year class; and ten sites (A, B, C, E, F, G, H, I, J, and M) to have had peaks in one or both of the 450 and 500 year classes. Ten sites (A, B, D, E, F, G, H, I, J, and N) had more than one peak, with up to 350 years between peaks. Nine sites (A, B, D, E, I, L, M, N, and O) had three or fewer *Thuja* older than 600 years.

Discussion

Age-Size Relationship

The age and size of the trees we observed agreed with those reported previously (Franklin and Hemstrom 1981, Beese and Sanford 1992, Keenan 1993). Although there was a general trend of increasing age with tree size, dbh was a poor predictor of tree age and the accuracy of predictions decreased with increasing tree size (Figure 1). Tree diameters provided general information about the range of tree ages on a site, as suggested by Keenan (1993), but diameter distributions did not clearly depict changes in *Thuja* populations with time. Inconsistent relationships between age and size have been shown for other species (e.g., Stewart 1986).

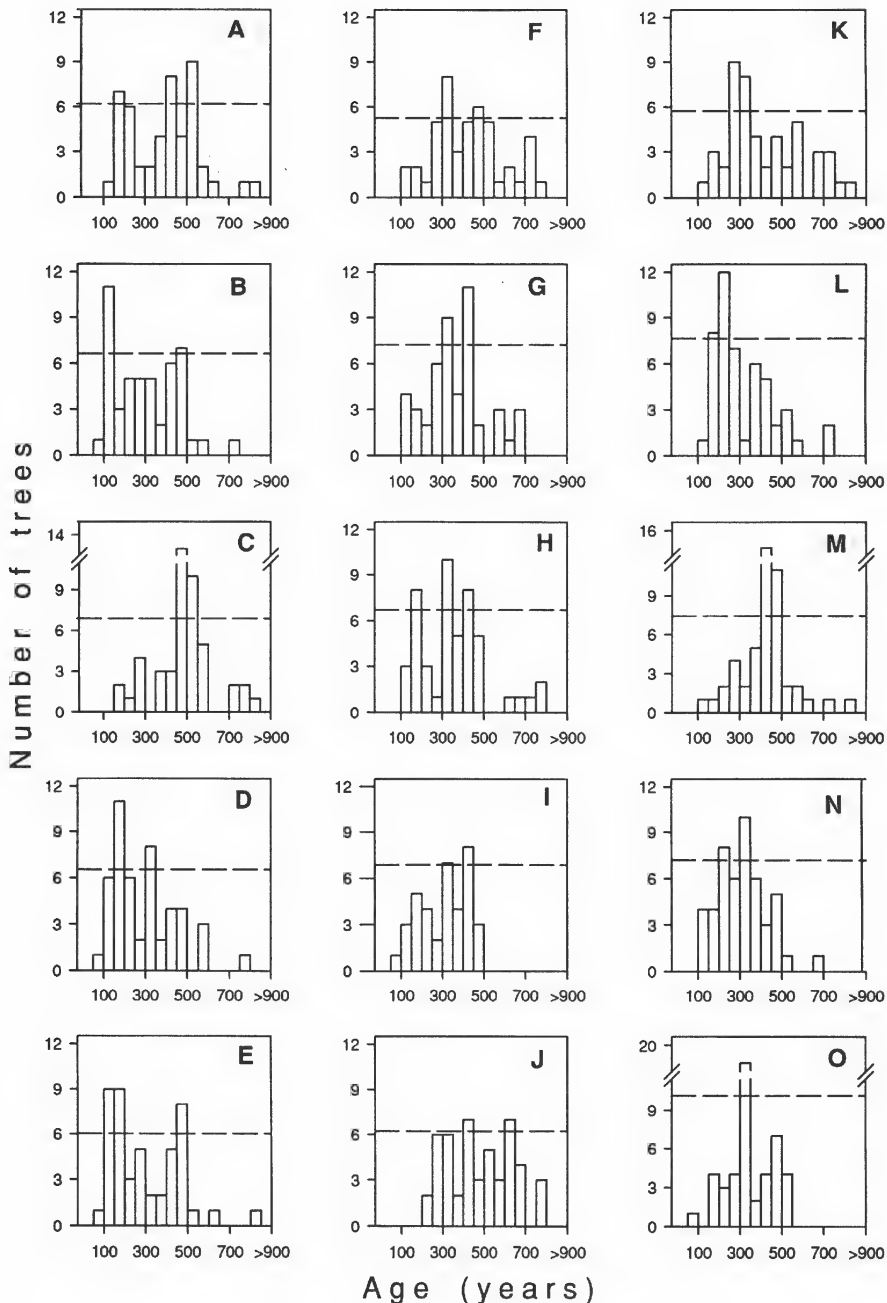


Figure 3. Age frequency distributions of *Thuja plicata* in the tree layer of study sites A to O. The x-axes labels show the upper limits of 50-year classes. The broken lines mark the mean class frequencies + 1 standard deviation of the mean; classes with frequencies above this line are "peak" classes.

Age Distributions

The low frequency of trees <100 years old resulted from the arbitrary minimum diameter of 7.5 cm used to define the tree layer of the sites and did not indicate a lack of regeneration on the sites. Delayed recruitment to the tree layer is consistent with *Thuja*'s tolerance of shade (Carter and Klinka 1992) and the slow replacement of canopy trees in old-growth forests in the coastal region (Lertzman and Krebs 1991, Spies et al. 1990).

The peaks in the age class distribution (Figures 2 and 3) indicated that establishment and mortality within *Thuja* populations have been variable during 800 years. From diameter distributions, it has been inferred that *Thuja* has low recruitment, but high survival in all size classes (Franklin and DeBell 1988, Keenan 1993). Theoretically, the corresponding age distributions should show high adult (canopy tree) survivorship with increased chance of death at the end of the life span. This theoretical distribution assumes that recruitment and mortality have been constant over time, *i.e.* that the population was at demographic equilibrium (Harcombe 1987). But, *Thuja* is evidently not at demographic equilibrium within the study area.

The age distributions of individual study sites (Figure 3) reflect sporadic mortality and regeneration episodes. They suggest the influence of disturbances of various magnitudes and extents. For example, disturbances of high intensity can reduce structural complexity by eliminating existing age classes in parts or all of a stand (Hemstrom and Franklin 1982). At least nine sites (A, B, D, E, I, L, M, N, and O) in the study area appeared to have been affected by such disturbances. Disturbances affecting stands *ca.* 600 to 700 years ago could explain the lack of *Thuja* trees greater than 600 years of age, although the life span of *Thuja* can be greater than 1000 years (Franklin and Hemstrom 1981, Keenan 1993).

In contrast to high intensity stand-level disturbances, small scale disturbances, such as windthrow, can facilitate continuous establishment and result in a spread of ages among trees (Beese and Sanford 1992) similar to those observed here. The predominant influence of wind in coastal old-growth forests in the region is becoming widely recognized (Lertzman and Krebs 1991, Spies et al. 1990). Moreover, the broad, flat, discontinuous distributions of diameters for *Thuja* from plots

of 0.25 to 0.4 ha (*e.g.* Gregory 1957, Keenan 1993) indicate the influence of small scale disturbances on *Thuja* dynamics. From these diameter distributions we can assume that the establishment of trees is intermittent (although exact years of establishment cannot be predicted with certainty), even at relatively small spatial scales.

Age Class Peaks

The irregular age class structures and occurrence of distinct peaks indicate that the conditions for *Thuja* regeneration within stands is variable through time. Interestingly, peaks occurred during the same 50-year classes at different sites and within different watersheds. This suggests that the conditions conducive to *Thuja* regeneration were effective at a local level and influenced a number of sites during the same periods. We offer three hypotheses relating these peak age classes to pulses of fire disturbance and climatic variation of the past.

Fire. We hypothesize that fire has influenced the study sites, altering stand structure and facilitating *Thuja* regeneration. The three periods of peak *Thuja* regeneration, 1491-1591, 1641-1691, and 1791-1841 are synchronous with high fire periods identified in the Pacific Northwest (Figure 4). During 1491-1591, "fire episodes," periods of high fire frequency (*sensu* Morrison and Swanson 1990), occurred in the Oregon Cascades (Cook-Quentin and Deer sites in Morrison and Swanson 1990) and major fires burned in mainland British Columbia (Eis 1962), Vancouver Island (Schmidt 1970), Desolation Peak (Agee et al. 1990) and Mount Rainier National Forest (Hemstrom and Franklin 1982). The 1450-1540 fire episode of the Olympic Peninsula (Henderson et al. 1989) overlaps with this period. During 1641 to 1691, fires burned in all of the cited areas, except the Deer site in Oregon. One major fire and three significant fires burned in the Bitterroot National Forest, and three significant fires burned in Yellowstone National Park during the same period (Table 2 in Heinzelman 1978). The most recent peak in *Thuja* age distributions concurs with high fire periods in the Oregon Cascades (Morrison and Swanson 1990), Mount Rainier National Forest (Hemstrom and Franklin 1982), Vancouver Island (Schmidt 1970) and the mainland of British Columbia (Eis 1962). The presence of charcoal in the soil, fire scarred trees, and the codominance

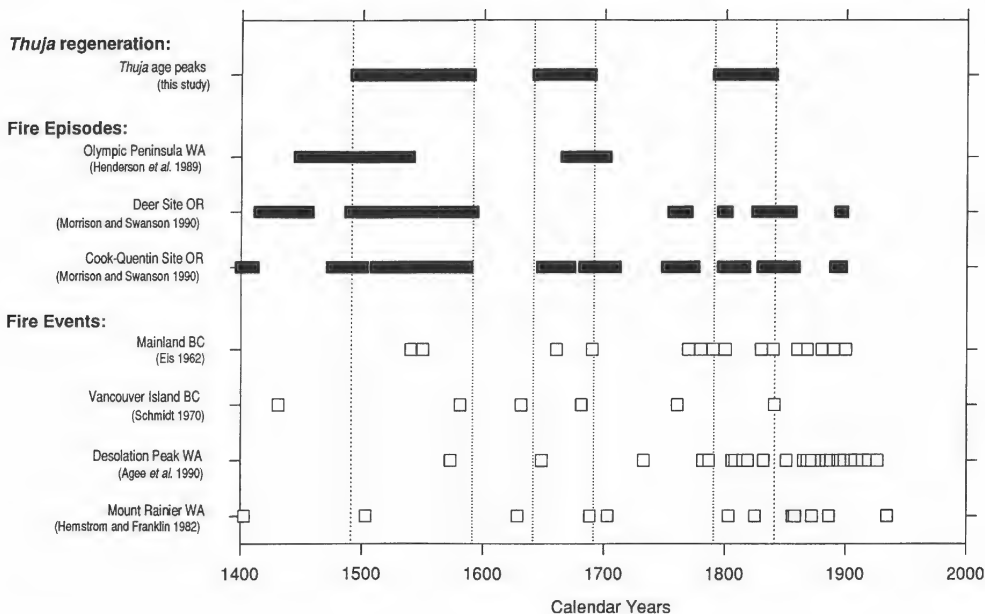


Figure 4. Chronology of *Thuja plicata* age peaks and fire disturbances in the Pacific Northwest. The left column identifies study areas and sources. Peak periods of *Thuja plicata* regeneration are represented by solid bars bounded by the vertical broken lines. Fire episodes greater than 1 year are represented by solid bars. Open squares show single years during which fires burned.

of intolerant *Pseudotsuga menziesii* in *Thuja* stands, provides strong evidence for our assertion that fire has affected the study area. However, we emphasize the need to document the fire history and fire regimes in the study area.

Climate. An alternate hypothesis to explain the observed age structures is the influence of a variable climate (Henderson and Brubaker 1986). Climate reconstruction from the Cascade Range, Washington (Graumlich and Brubaker 1986) show three periods of cooler than average summer temperatures (1600-1650, 1700-1760, and 1860-1900), each punctuating the periods of high *Thuja* establishment (Figures 2 and 4). Cooler climate might have reduced the success of *Thuja* establishment and recruitment, resulting in relatively low frequencies in corresponding age classes. It is evident from the current elevation distribution of *Thuja* and its decreasing vigour and abundance in montane forests, that cooler climate and shorter growing seasons are not conducive to *Thuja* establishment and growth (Minore 1990). Moreover, dendroecological findings from the study area show di-

ameter growth of *Thuja* is significantly affected by temperature (Dobry et al. in press). As the climatic variations identified by Graumlich and Brubaker (1986) probably affected a large region (Brubaker 1980), including our study area, we cannot discount the influence of historic climate variation on *Thuja* demographics.

Climate-Fire Interaction. A third hypothesis is that climate and fire interact and have affected *Thuja* demographics, now reflected in age structures. A relationship between climate and fire episodes in the Pacific Northwest has been postulated by Franklin et al. (1988), Hemstrom and Franklin (1982), Henderson et al. (1989), and Agee (1993). But the nature of the climate-fire relationship remains unclear. For example, high intensity fires ca. 600 to 700 years ago have been attributed to the warmer drier climate of the Medieval Optimum (1000-1300, Henderson et al. 1989), while other authors report cooling trends associated with low sunspot activity which are synchronous with fire periods (e.g. Agee 1993, Henderson et al. 1989).

Conclusions

From age frequency distributions, we have shown that the populations of *Thuja* in the study area were uneven-aged but were not in demographic equilibrium. We conclude that single-tree to stand-level disturbances were manifest in the age distributions. Considering the longevity of *Thuja* and the spatio-temporal scales at which wind, fire and climate affect the forests within the Pacific Northwest, it is improbable that *Thuja* will arrive at demographic equilibrium within the study area, even after long periods. Better knowledge of disturbance history and disturbance regimes within British Columbia's coastal forests are

needed to improve our understanding of *Thuja* population dynamics.

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Literature Cited

- Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC. 493 p.
- Agee, J. K., M. Finney, and R. de Gouvenain. 1990. Forest fire history of Desolation Peak, Washington. Can. J. For. Res. 20: 350-356.
- Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification, 2nd ed. Agric. Can. Publ. 1646. Ottawa, ON 164 p.
- Beese, W. J. and J. S. Sanford. 1992. Age of old-growth forests on Vancouver Island. LUPAT Contract #98444, MacMillan Bloedel Ltd. Nanaimo, B.C. 19 p.
- Brubaker, L. B. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. Ecology 61:798-807.
- Carter, R. E. and K. Klinka. 1992. Variation in the shade tolerance of Douglas-fir, western hemlock, and western redcedar in coastal British Columbia. For. Ecol. Manage. 55:87-105.
- Daniels, L. D. 1994. Natural regeneration dynamics of western redcedar in coastal forests. In Baumgartner, D. M., J. E. Lotan, and J. R. Tonn (eds.) Interior Cedar-Hemlock-White Pine Forests: Ecology and Management Conf. Proc., March 2-4 1993. Washington State Univ., Pullman, WA. pp. 319-326.
- Demaerschalk, J. P. and S. A. Y. Omule. 1978. Stump and breast height diameter tables for the British Columbia merchantable trees species. Fac. For., Univ. British Columbia, Vancouver, BC.
- Dobry, J., J. Kencl, K. Klinka and B. A. Blackwell. (in press). Climate signals in coastal old-growth forest trees near Vancouver, British Columbia. Radiocarbon.
- Eis, S. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. Forestry Bull. No.4. Fac. For., Univ. British Columbia, Vancouver, BC. 76 p.
- Franklin, J. F. and D. S. DeBell. 1988. Thirty-six years of tree population change in old-growth *Pseudotsuga-Tsuga* forest. Can. J. For. Res. 18:633-639.
- Franklin, J. F. and M. A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D. C., H. H. Shugart and D. B. Bodkin (eds.). Forest Succession: Concepts and Application. Springer-Verlag, New York. pp. 212-229.
- Franklin, J. F., W. M. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The forest communities of Mount Rainier National Park. USDA Forest Service PNW Res. Stn., Portland, OR. 194 p.
- Graumlich, L. J. and L. B. Brubaker. 1986. Reconstruction of annual temperature (1590-1979) for Longmire, Washington, derived from tree rings. Quaternary Res. 25:223-234.
- Gregory, R. A. 1957. Some silvicultural characteristics of western redcedar in southeast Alaska. Ecology 38:646-649.
- Harcombe, P. A. 1987. Tree life tables. BioSci. 37:557-568.
- Heinselman, M. L. 1978. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In Mooney, H. A., T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners (eds.). Fire Regimes and Ecosystem Properties, Conf. Proc., December, 1978. Honolulu, Hawaii. pp. 7-57.
- Hemstrom, M. A. and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Res. 18:32-51.
- Henderson, J. A. and L. Brubaker. 1986. Responses of Douglas-fir to long-term variations in precipitation and temperature in western Washington. In Oliver, C. D., D. P. Hanley and J. A. Johnson (eds.). Douglas-fir: Stand Management for the Future. Contribution No. 55, Inst. For. Res., Univ. Washington, Seattle, WA. pp. 162-167.
- Henderson, J. A., D. H. Peter, R. D. Leshner and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. R6-ECOL-TP 001-88, USDA Forest Service, PNW Region. 502 p.
- Keenan, R. J. 1993. Structure and function of western redcedar and western hemlock forests on northern Vancouver Island. Ph.D. Thesis, Fac. For., Univ. British Columbia, Vancouver, BC. 167 p.
- Klinka, K., V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of coastal British Columbia. Univ. of British Columbia Press, Vancouver B.C. 288 p.
- Klinka, K., J. Pojar and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. Northwest Sci. 65:32-47.
- Lertzman, K. P. and C. J. Krebs. 1991. Gap-phase structure of a sub-alpine old growth forests. Can. J. For. Res. 21:1730-1741.

- Lorimer, C. G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15:200-213.
- Luttmerding, H. A., D. A. Demarchi, E. C. Lea, D. V. Meidinger and T. Vold. 1990. Describing Ecosystems in the Field, 2nd ed. MOE Manual 11, British Columbia Ministry of Environment, Lands and Parks, Victoria, BC. 213 p.
- Minore, D. 1990. *Thuja plicata* Donn ex D. Don. In Burns, R. M. and B. H. Honkala (eds.). *Silvics of North America: 1. Conifers. Agriculture Handbook 654*, USDA Forest Service, Washington, DC. pp. 590-600.
- Morrison, P. H. and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. Gen. Tech. Rep. PNW-GTR-254. USDA Forest Service. Pac. Northwest For. and Range Exp. Stn., Portland, OR 77 p.
- Oliver, C. D., M. N. Nystrom and D. S. DeBell. 1988. Coastal stand silvicultural potential for western redcedar. In Smith, N. J. (ed.) *Western red cedar—does it have a future?* Conf. Proc., July 13-14, 1987. Fac. Forestry, Univ. British Columbia, Vancouver, BC. pp. 39-46.
- Schmidt, R. L. 1955. Some aspects of western redcedar regeneration in the coastal forests of British Columbia. B.C. Department of Lands and Resources, Research Notes No. 29. Victoria, B.C. 10 p.
- _____. 1970. A history of pre-settlement fires on Vancouver Island as determined from Douglas-fir ages. In Smith, J. H. G. and J. Worrall (eds.) *Tree-ring analysis with special reference to northwestern America*. Forestry Bull. No. 7, Fac. For., Univ. British Columbia, Vancouver, BC. pp. 107-108.
- Spies, T. A., J. F. Franklin and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20:649-658.
- Stewart, G. H. 1986. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. *Ecology* 67:534-544.
- Veblen, T. T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. *Bull. Torr. Bot. Club* 113:225-240.
- Zar, J. H. 1984. *Biostatistical Analysis*. 2nd ed. Prentice-Hall, New Jersey. 718 p.

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Autecology of Mosses in Coniferous Forests in the Central Western Cascades of Oregon

Abstract

Forest mosses contribute to nutrient cycling, provide food and nesting materials to small animals, and serve as biological indicators. In addition, the harvest of moss as a special forest product has grown in recent years in the Pacific Northwest. To quantify certain ecological characteristics of moss species, we examined substrate and forest community affinities in the central western Cascades of Oregon. Cover and frequency of individual species were measured on the forest floor, logs, and tree bases in *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Abies amabilis* Dougl. ex Forbes forest communities. Thirty moss species were found, representing 21 genera and 13 families. Common substrates for individual moss species were identified on the basis of frequency values. Mosses comprise a substantial portion of the vegetative biological diversity in forest ecosystems in the Cascades. A better understanding of moss autecology will assist resource managers in protecting this important source of diversity.

Introduction

Understanding the patterns of distribution and abundance of individual species is necessary for understanding ecosystem structure and function and for ensuring proper management. In forests, mosses are a critical component of nutrient cycling, serving as sinks that capture and then leach nutrients back into the ecosystem (Turner and Long 1975, Rieley et al. 1979). Mosses and other bryophytes provide food and nest material to invertebrates and vertebrates (Forest Ecosystem Management Assessment Team (FEMAT) 1993). Furthermore, mosses serve as indicators of environmental change in forest communities (Schofield 1988, Vitt 1990) and have economic value as forest products used in the floral industry (Peck 1990, Schlosser et al. 1992). To augment understanding of the ecology of individual species, we examined mosses on the forest floor, on the upper surface of downed logs, and on tree bases in forest stands in the central western Cascades of Oregon on and near the H. J. Andrews Experimental Forest.

For the most part, information on suitable substrates for moss species in the Pacific Northwest is limited to floristic works (Steele 1978), taxonomic keys (Schofield 1969, Lawton 1971, Flowers 1973, Schofield 1976), and anecdotal accounts in field guides (Vitt et al. 1988). This study quantifies local distribution patterns and

substrate affinities to a greater extent than previous studies in the same geographic area (e.g., Pike et al. 1975, Hawk et al. 1978, Binkley and Graham 1981). Several habitats and their associated species were not included in our study (e.g., cliffs, sides of logs, tree limbs, tree canopies; see Pike et al. 1975). Nomenclature follows Anderson et al. (1990).

Study Area

Observations were made in 15 permanent 0.25-ha forest study areas in and near the H. J. Andrews Experimental Forest (Hawk et al. 1978, Franklin and Van Pelt 1990) near Blue River, Oregon, in the western Cascades. These sites were chosen to span the range of the environmental gradient discussed by Zobel et al. (1976), extending from warm and dry to cold and wet sites. Four of the 15 sites were mature forest, 130 to 150 years old, and the other 11 sites were old-growth forest, more than 400 years old.

Vegetation of the warm and dry sites (elevations 510 to 1060 m) was dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with oceanspray (*Holodiscus discolor* (Pursh) Maxim.) in the understory. On the driest intermediate sites on the environmental gradient, vegetation was dominated by Douglas-fir. On less dry intermediate sites, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was also present, and the wettest

intermediate sites also had Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) co-dominants. All intermediate sites were between 490 and 950 m elevation; vine maple (*Acer circinatum* Pursh), western swordfern (*Polystichum munitum* (Kaulf.) Presl), Oregon oxalis (*Oxalis oregana* Nutt.), and twinflower (*Linnaea borealis* L.) were common understory species. Vegetation of the cold and wet sites (1020 to 1570 m) was dominated by Pacific silver fir with Alaska huckleberry (*Vaccinium alaskaense* Howell) and bunchberry (*Cornus canadensis* L.) or coolwort (*Tiarella trifoliata* L. var. *unifoliata* (Hook.) Kurtz.) in the understory.

Methods

Sampling took place from June to August, 1991. Cover was estimated visually to the nearest 1% (within a 20- by 50-cm Daubenmire (1959) frame) for each species on 30 microplots on the forest floor, 30 on logs, and 15 on tree bases at each of the 15 sites. The Daubenmire frame was systematically placed on the forest floor (with logs and rocks avoided) every 5 m along three parallel transects within a 50-m² plot. Frames were also placed on downed logs that had just begun to lose some of their bark; logs were chosen so that decay was as uniform as possible. Because bryophyte communities on the tops and sides of logs differ, only the upper surface was sampled. Finally, frames were placed to lean against the bases of overstory trees (with the 20-cm side down); the north side of trees was arbitrarily chosen for consistency. Cover was then averaged by species and substrate for all microplots within a site. Pearson correlation coefficients were used to assess the relationship between elevation and total cover of each species in each stand. Constancy was computed as the percentage of sites in which a species occurred out of the 15 sites examined.

Frequency on each substrate at each site was computed as the percentage of microplots containing the species divided by the total number of microplots for the substrate and site. Species substrate affinities were assigned only when average cover across all sites was greater than 1%. Substrate affinities are shown for species that occur on one substrate at least twice as often as on the next most common substrate. These substrate rankings were based on the species' frequency on that substrate across all sites.

Vouchers were deposited in the Oregon State University Herbarium, Corvallis, Oregon.

Results

We encountered 13 families, 21 genera, and 30 species of mosses (Table 1). Some species were quite widespread and abundant, while others were more narrowly distributed and rare (Table 2). Species in Table 2 are listed in order of their correlation coefficients with elevation, starting with species with low cover at high elevations. *Isoetecium myosuroides*, *Hypnum circinale*, *Polytrichum juniperinum*, and *Eurhynchium oreganum* all had strong negative correlations with elevation. *Plagiothecium laetum* and *Roellia roellii*, however, showed the opposite tendency, with strong positive correlations with elevation.

Hypnum circinale and *Dicranum fuscescens* occurred across the entire elevational range, on all sites sampled, and on all three substrates. *Dicranum tauricum*, *Rhizomnium glabrescens*, *Rhytidiadelphus triquetrus*, and *Plagiothecium laetum* also had broad elevational ranges and occurred on all substrates, but they were absent from some sites. Despite their broad elevational ranges, *Aulacomnium androgynum* and *Atrichum selwynii* occurred on few sites and not all substrates.

Isoetecium myosuroides, *Eurhynchium oreganum*, and *Dicranum scoparium* were found at most sites of low to moderate elevation and occurred on all substrates. *Homalothecium megaptilum*, *Rhytidiopsis robusta*, *Antitrichia curtipendula*, *Hylacomium splendens*, and *Rhytidiadelphus loreus* occurred on logs and the forest floor at low to moderate elevations and were less frequently encountered. *Claopodium crispifolium* did not occur above 830 m but was found on all three substrates.

Polytrichum juniperinum, *Polytrichadelphus lyallii*, *Eurhynchium praelongum*, and *Claopodium whippleanum* each were encountered on only two sites at relatively low elevation and occurred primarily on the forest floor. *Scleropodium touretei*, *Racomitrium heterostichum*, *Metaneckera menziesii*, *Plagiothecium undulatum*, *R. canescens*, *R. aciculare*, *Plagiomnium insigne*, *Leucolepis menziesii*, and *Roellia roellii* each occurred in only one site and were rare where they did occur.

TABLE 1. Mosses on the forest floor, logs, and tree bases in coniferous forests of the central western Cascades of Oregon.

Species name, authority	Family	Growth form ¹
<i>Aulacomnium androgynum</i> (Hedw.) Schwaegr.	Aulacomniaceae	A
<i>Eurhynchium oreganum</i> (Sull.) Jaeg.	Brachytheciaceae	P
<i>Eurhynchium praelongum</i> (Hedw.) B.S.G.	Brachytheciaceae	P
<i>Homalothecium megaptilum</i> (Sull.) Schof.	Brachytheciaceae	P
<i>Isothecium myosuroides</i> Brid.	Brachytheciaceae	P
<i>Scleropodium touretii</i> (Brid.) L. Koch	Brachytheciaceae	P
<i>Roellia roellii</i> (Broth.) Andr. in Crum	Bryaceae	A
<i>Dicranum fuscescens</i> Turn.	Dicranaceae	A
<i>Dicranum scoparium</i> Hedw.	Dicranaceae	A
<i>Dicranum tauricum</i> Sapehin.	Dicranaceae	A
<i>Racomitrium aciculare</i> (Hedw.) Brid.	Grimmiaceae	A
<i>Racomitrium canescens</i> (Hedw.) Brid.	Grimmiaceae	A
<i>Racomitrium heterostichum</i> (Hedw.) Brid.	Grimmiaceae	A
<i>Hylocomium splendens</i> (Hedw.) B.S.G.	Hylocomiaceae	P
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.	Hylocomiaceae	P
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.	Hylocomiaceae	P
<i>Hypnum circinale</i> Hook.	Hypnaceae	P
<i>Plagiothecium laetum</i> B.S.G.	Hypnaceae	P
<i>Plagiothecium undulatum</i> (Hedw.) B.S.G.	Hypnaceae	P
<i>Claopodium crispifolium</i> (Hook.) Ren. & Card.	Leskeaceae	P
<i>Claopodium whippleanum</i> (Sull.) Ren. & Card.	Leskeaceae	P
<i>Antitrichia curtipendula</i> (Hedw.) Brid.	Leucodontaceae	P
<i>Leucolepis menziesii</i> (Hook.) Steere	Mniaceae	A
<i>Plagiomnium insigne</i> (Mitt.) T. Kop.	Mniaceae	P
<i>Rhizomnium glabrescens</i> (Kindb.) T. Kop.	Mniaceae	A
<i>Metaneckera menziesii</i> (Hook.) Steere	Neckeraceae	P
<i>Atrichum selwynii</i> Aust.	Polytrichaceae	A
<i>Polytrichadelphus lyallii</i> Mitt.	Polytrichaceae	A
<i>Polytrichum juniperinum</i> Hedw.	Polytrichaceae	A
<i>Rhytidiopsis robusta</i> (Hook.) Broth.	Rhytidiaceae	P

¹Growth form (Lawton 1971):

A = Acrocarp (erect plant with terminal capsules)

P = Pleurocarp (spreading plant with capsules on lateral branches)

Fifteen of the 30 species were abundant enough that substrate affinities could be assessed (Table 2). Species exhibiting affinities for the forest floor

included *Polytrichum juniperinum*, *Eurhynchium praelongum*, *Homalothecium megaptilum*, and *Aulacomnium androgynum*. *Rhytidiopsis robusta*,

TABLE 2. Habitat and substrate distributions, listed in order of increasing correlation with elevation.

Species name	Elev. (m)		Correlation with elevation	Constancy (%)	Frequency class by substrate			Substrate affinity
	Min.	Max.			Floor	Log	Tree	
<i>Isoetecium myosuroides</i>	490	1060	-.4974	73	3	1	4	Generalist
<i>Hypnum circinale</i>	490	1570	-.4855	100	3	4	5	Trees (Logs)
<i>Polytrichum juniperinum</i>	510	680	-.4623	13	2	1	0	Floor
<i>Eurhynchium oreganum</i>	490	1060	-.4551	80	5	4	4	Generalist
<i>Polytrichadelphus lyallii</i>	510	680	-.3777	13	1	1	0	
<i>Dicranum fuscescens</i>	490	1570	-.3282	100	4	4	5	Trees
<i>Claopodium crispifolium</i>	510	830	-.2429	27	2	2	1	
<i>Eurhynchium praelongum</i>	490	510	-.2087	13	2	1	1	Floor
<i>Homalothecium megaptilum</i>	510	1060	-.2066	33	3	1	0	Floor
<i>Scleropodium toureteii</i>	510	510	-.1959	7	1	0	0	
<i>Rhytidiopsis robusta</i>	490	1020	-.1793	33	1	2	0	Logs
<i>Racomitrium heterostichum</i>	670	670	-.1690	7	0	1	0	
<i>Antitrichia curtipendula</i>	520	830	-.1396	20	1	1	0	
<i>Metaneckera menziesii</i>	720	720	-.1311	7	1	1	1	
<i>Hylocomium splendens</i>	490	670	-.1299	33	2	1	0	
<i>Dicranum scoparium</i>	490	950	-.1092	53	2	2	3	Generalist
<i>Dicranum tauricum</i>	510	1570	-.1001	73	2	3	2	Logs
<i>Aulacomnium androgynum</i>	510	1570	-.0913	27	2	1	0	Floor
<i>Rhizomnium glabrescens</i>	490	1440	-.0773	47	2	3	2	Logs
<i>Plagiothecium undulatum</i>	830	830	-.0476	7	1	1	0	
<i>Rhytidiadelphus loreus</i>	490	830	-.0476	13	1	1	0	
<i>Racomitrium canescens</i>	680	680	.0000	7	1	0	0	
<i>Racomitrium aciculare</i>	950	950	.0146	7	1	1	0	
<i>Rhytidiadelphus triquetrus</i>	490	1570	.0291	73	3	3	2	Generalist
<i>Plagiomnium insigne</i>	950	950	.0435	7	0	1	0	
<i>Claopodium whippleanum</i>	670	830	.1194	13	1	0	0	
<i>Leucolepis menziesii</i>	1060	1060	.1270	7	0	1	0	
<i>Atrichum selwynii</i>	510	1570	.2681	13	1	0	0	
<i>Roellia roellii</i>	950	950	.4155	7	1	1	0	
<i>Plagiothecium laetum</i>	490	1570	.6438	60	3	3	2	Generalist

Frequency codes: 0 = 0%

1 = 0.1–1.0

2 = 1.1–5.0

3 = 5.1–10.0

4 = 10.1–50.0

5 = 50.1–100.0

Dicranum tauricum, and *Rhizomnium glabrescens* showed an affinity for logs. *Dicranum fuscescens* occurred most commonly on tree bases. *Hypnum circinale* occurred on tree bases nearly twice as often as on logs and occurred on the forest floor less than one-tenth as often as on tree bases. Those species listed as generalists had similar frequencies for each of the three substrates.

Discussion

Basic ecological information for mosses is one requirement for ecologically sustainable forest management (FEMAT 1993). Currently, however, moss ecology is poorly understood. In part, this is because of the tremendous variability among moss species and their flexibility as poikilohydric cryptogams. Thus the habits and habitats of some species may vary from one geographic region to the next, and possibly from one microsite to the next.

Ecological observations from farther north in the Pacific Northwest indicate patterns that differ from those found for some of the same species in this study. On the Olympic Peninsula, *Hypnum circinale* and *Dicranum fuscescens* attain their greatest abundance in relatively mesic areas (Hoffman and Kazmierski 1969). In this study these species were almost equally abundant in warm and dry and cold and wet sites. Differences in sampling protocols may have contributed to this discrepancy; tree bases up to 4 m were sampled in the Olympic Peninsula study, which allowed the authors to observe that, as Szczawinski (1953) proposed, bryophytes in mesic areas are displaced further up the trunks of trees than in more xeric areas. Our sampling only extended up tree bases to 50 cm, which appears to be too small a gradient to show this phenomenon.

In British Columbia, *Dicranum tauricum* occurs on logs and *Plagiomnium insigne* on moist earth and tree bases (Schofield 1976). However, we found *D. tauricum* on all three substrates (although primarily on logs) and *P. insigne* only on logs. In addition, we found *Polytrichadelphus lyallii* on the forest floor and logs in low-elevation stands. Lawton (1971) reports this species as occurring on soil at high elevations (1200 m to 3300 m and higher).

In our area, Lawton (1971) reported elevational zonation for four of the moss species we encountered. Our findings agree with these regional de-

scriptions. We found *Claopodium crispifolium*, *Plagiomnium insigne*, and *Plagiothecium laetum* within the elevational ranges described by Lawton (1971), but *Dicranum fuscescens* occurred at all elevations up to and including our highest site at 1570 m, 570 m higher than Lawton (1971) describes. This is in keeping with the findings of Bellolio-Trucco and Ireland (1990), who reported *D. fuscescens* to be very widespread in Quebec with populations occurring over a broad geographic area as well as on varying substrates. This species, along with *Hypnum circinale*, showed a strong affinity for tree bases and was very abundant in our stands. Other studies of tree base habitats in the Pacific Northwest have also found these species to be among the most frequently encountered (Hawk et al. 1978, Hoffman and Kazmierski 1969).

Higher-elevation stands had a lower abundance of *Isoetecium myosuroides*, *Hypnum circinale*, *Polytrichum juniperinum*, and *Eurhynchium oregonum*. The absence of *P. juniperinum* at higher elevations is inconsistent with the reported phenotypic plasticity of this species; in other areas it is known to adapt to the altered climatic conditions along elevational gradients (Bazzaz et al. 1970). The other three species are present on all substrates in most stands. Their distributions may reflect an extension to higher-elevation stands of the "similar gradient hypothesis" proposed by McCune (1993). High-elevation *Abies* stands are structurally different from lower-elevation *Pseudotsuga* and *Tsuga* forests, with lower canopies and smaller-diameter trees (Franklin 1988). This structure can be considered comparable to that of young *Pseudotsuga* forests, which have a lower biomass of bryophytic epiphytes than older, more structurally complex stands (McCune 1993). However, the reduction in moss abundance in higher-elevation stands may also be a function of reduced temperatures, greater snowpacks, and less free water during the growth season, as well as other factors that were not measured in this study.

Two species, however, showed strong positive associations with elevation. *Roellia roellii* was present in only one stand and thus did not change in abundance with increasing elevation. This species, which occurred at 950 m elevation, has been noted previously in stands of approximately 1000 m (D. Norris, D. Wagner, pers. comm.). *Plagiothecium laetum*, found on all substrates in all stands, showed a marked increase in abundance

with increasing elevation. This distribution supports its description in Lawton (1971) as a very variable species occurring on a wide range of habitats, and in particular in high-elevation (>700 m) coniferous forests.

Several species that most commonly occur as epiphytes were found well established on the forest floor (*Isoetecium myosuroides*, *Claopodium crispifolium*, *Antitrichia curtipendula*, *Metaneckera menziesii*). Although it is impossible to determine whether these populations began their development while epiphytic, all were clearly established on the forest floor and apparently thriving. The reestablishment of these epiphytes on the forest floor is common throughout the Pacific Northwest and has been previously noted by Lawton (1971) and Schofield (1976).

Six of the species in this study were identified by FEMAT (1993) as "closely associated with late-successional or old-growth forests" and described as dependent on particular habitats within such forests. *Hypnum circinale* and *Dicranum fuscescens* were most common on tree bases in this study, consistent with the FEMAT report. Similarly, *Rhizomnium glabrescens* was most common on logs, although it was not found exclusively on decaying wood as stated in the report. We found *Rhytidiopsis robusta*, on the other hand, to be most common on logs, whereas the FEMAT report described it as a species of shaded duff and humic soil. Two other species included in the FEMAT report, *Plagiothecium undulatum* and *Roellia roellii*, were each encountered in only one of our sites.

The classification of substrate affinities is intended to serve as a general guide for species distributions in our area. Classifications of this sort are useful when habitats and substrates are managed for specific goals such as promoting biodiversity. Other studies in the central western Cascades of Oregon indicate that additional moss species occur on the substrates we sampled. These include *Dicranoweisia cirrata* and *Barbula* sp. on tree bases (Pike et al. 1975), and *Claopodium bolanderi* and *Mnium* sp. (Hawk et al. 1978) on the forest floor. However, *C. bolanderi* and *C.*

crispifolium are difficult to distinguish in the field. Thus it is possible that both species were present and only one was recognized by each set of researchers. Further, Hawk et al. (1978) may have classified *Plagiomnium insigne* as *Mnium* sp.

Generalizations about moss species distributions are best made and utilized on a regional basis where geographic and climatic variables are relatively consistent. Although it would be difficult to manage for individual moss species, given their broad distributions and the paucity of ecological data, information on moss groups associated with certain habitats or forest communities allows managers to operate on a larger scale. With the increased harvest of moss as a forest product in western Oregon, ecological information of this kind should facilitate sustainable management. Understanding moss species distribution patterns may allow managers to regulate for groups of species and to anticipate which species will be targeted by the floral industry. Both ecosystem science and sustainable management of forest mosses will be furthered if the ecology of western forest mosses and the impact of harvest on these mosses and the forest ecosystem are investigated.

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Literature Cited

- Anderson, L. E., H. A. Crum, and W. R. Buck. 1990. List of the mosses of North America north of Mexico. *The Bryologist* 93:448–499.
- Bazzaz, F. A., D. J. Paolillo, and R. H. Jagels. 1970. Photosynthesis and respiration of forest and alpine populations of *Polytrichum juniperinum*. *The Bryologist* 73:579–585.
- Bellolio-Trucco, G., and R. R. Ireland. 1990. A taxonomic study of the moss genus *Dicranum* (Dicranaceae) in Ontario and Quebec. *Can. J. Bot.* 68:867–909.
- Binkley, D., and R. L. Graham. 1981. Biomass, production, and nutrient cycling of mosses in an old-growth Douglas-fir forest. *Ecology* 62:1387–1389.
- Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northw. Sci.* 33:43–61.
- Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. USDA; USDI (and others), Portland, Oregon.
- Flowers, S. 1973. Mosses: Utah and the West. Brigham Young University Press, Provo, Utah. 567 p.
- Franklin, J. F. 1988. Pacific Northwest Forests, in M. G. Barbour and W. D. Billings (eds.) *North American Terrestrial Vegetation*, Cambridge U. Press, Cambridge. Pp. 104–130.
- Franklin, J., and R. Van Pelt. 1990. Old growth reference stand network in the Pacific Northwest: recording long-term ecosystem dynamics. *Northwest Environ. J.* 6:423–424.
- Hawk, G. M., J. F. Franklin, W. A. McKee, and R. B. Brown. 1978. H. J. Andrews Experimental Forest reference stand system: establishment and use history. U.S./International Biological Program, Coniferous Forest Biome Ecosystem Analysis Studies, Bull. 12, University of Washington, Seattle, Washington.
- Hoffman, G. R., and R. G. Kazmierski. 1969. An ecologic study of epiphytic bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington I. Description of the vegetation. *The Bryologist* 72:1–19.
- Lawton, E. 1971. Moss Flora of the Pacific Northwest. The Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan. 362 p.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *The Bryologist* 96:405–411.
- Peck, J. E. 1990. The harvest of moss: an industrial perspective. Res. Rep. Dept. of Sociology and Anthropology, Linfield College, McMinnville, Oregon. 20 p.
- Pike, L. H., W. C. Denison, D. M. Tracy, M. A. Sherwood, and F. M. Rhoades. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *The Bryologist* 78:309–402.
- Rieley, J. O., P. W. Richards, and A. D. L. Bebbington. 1979. The ecological role of bryophytes in a North Wales woodland. *J. Ecol.* 67:497–527.
- Schlosser, W. E., K. A. Blatner, and B. Zamora. 1992. Pacific Northwest forest lands potential for floral greenery production. *Northw. Sci.* 66:44–55.
- Schofield, W. B. 1969. Some Common Mosses of British Columbia. British Columbia Provincial Museum Handbk. No. 28. Victoria, B.C. 262 p.
- . 1976. Bryophytes of British Columbia III: Habitat and distributional information for selected mosses. *Syesis* 9:317–354.
- . 1988. Bryogeography and the bryophytic characterization of biogeoclimatic zones of British Columbia, Canada. *Can. J. Bot.* 66:2673–2686.
- Steele, A. 1978. Bryophyte communities of central Idaho forests. *Northw. Sci.* 52:310–322.
- Szczawinski, A. 1953. Corticolous and lignicolous communities in the forest associations of the Douglas-fir forest on Vancouver Island. Ph.D. dissertation, University of British Columbia, Vancouver.
- Turner, J., and J. N. Long. 1975. Accumulation of organic matter in a series of Douglas-fir stands. *Can. J. For. Res.* 5:681–690.
- Vitt, D. H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical, and topographic gradients. *Bot. J. Linn. Soc.* 104:35–59.
- Vitt, D. H., J. E. Marsh, and R. V. Bovey. 1988. Mosses, Lichens & Ferns of Northwest North America. Lone Pine Publishing, Edmonton, Alberta. 296 p.
- Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs* 46:135–156.

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Effects of Grazing by Ungulates on Upland Bunchgrass Communities of the Northern Winter Range of Yellowstone National Park

Abstract

Herbivory by native ungulates, primarily elk (*Cervus elaphus*), was studied on xeric, bunchgrass-dominated slopes on the Northern Yellowstone ungulate winter range of Yellowstone National Park. Plant cover, standing green biomass, and nutrient concentrations were compared between grassland sites protected from grazing for 24–27 years and adjacent plots grazed mostly during winter by elk, and to some extent by bison (*Bison bison*). Accumulated litter and standing dead vegetation were four times more abundant on the ungrazed plots. However, few consistent differences were observed in grass or forb biomass from elk herbivory. There was no overall effect of grazing treatment on forbs or other nongrasses ($P < 0.05$). Total grass biomass was less on grazed than ungrazed sites in 1986, after a dry, warm spring, but there was no difference in 1987 ($P < 0.05$). Biomass of junegrass (*Koeleria cristata*) and thick-spiked wheatgrass (*Agropyron dasystachyum*) was greater on grazed than ungrazed sites. Three nongrasses (*Artemisia frigida*, *Phlox hoodii*, *Antennaria microphylla*) were more abundant on some ungrazed sites although the effect on grazing treatment was not significant ($P > 0.05$). The numbers of grasses ($n = 4.5$), forb ($n = 17.5$) and shrub ($n = 3.5$) species did not differ between grazed and ungrazed plots ($P < 0.05$). Vegetative culms of bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), bluegrasses (*Poa spp.*), needle-and-thread grass (*Stipa comata*), junegrass, and thick-spiked wheatgrass were shorter on winter grazed plots ($P < 0.05$), but grazing did not affect the numbers of vegetative culms or the height or numbers of reproductive culms of grasses ($P > 0.05$), with the single exception that more vegetative culms of junegrass occurred on grazed sites. Protein content averaged 16% higher in bluebunch wheatgrass, 36% higher in Idaho fescue, and 10% higher in junegrass ($P < 0.05$) on grazed sites. Bare ground averaged 38% more on grazed sites than on ungrazed sites ($P < 0.05$), but pebble cover was 50% less on grazed sites (probably because of hoof compaction); as a result all bare surfaces (bare ground plus pebble cover) averaged only 18% greater on grazed sites. Dead clumps of the grazing sensitive bluebunch wheatgrass and Idaho fescue can be expected on an overgrazed range, but dead bunchgrass clumps did not vary between grazed and ungrazed sites ($P < 0.05$). The effects of herbivory by native ungulates was observed in swale sites that had been disturbed by agricultural activities until the 1930s. Three grasses (*Stipa viridula*, *Poa pratensis*, *P. compressa*) possessed greater cover on grazed swales, but one forb, field pennycress (*Thlaspi arvensi*), was less abundant on grazed sites. Herbivory by native ungulates greatly stimulated grass but not forb cover on these productive swale sites (grass cover was double that of ungrazed sites) ($P < 0.05$), and grazing mostly by elk contributed to the continued dominance of these sites by the exotic, grazing resistant *Poa pratensis* even 54 years following cessation of agricultural activities.

Introduction

Caughley (1970, 1976, 1979) and Sinclair (1977) suggested that free-ranging ungulates reach an equilibrium with their vegetative food base. Beginning in 1967, Yellowstone National Park embarked upon an experimental program of “hands-off” or natural regulation management of the large ungulates within the park’s boundaries (Cole 1971, Houston 1976), although harvest of migratory elk north of the park was encouraged to the greatest extent possible. Cole (1971) stated that over a period of years, naturally regulated ungulate populations were self regulating units. Yellowstone ungulates regulated their own mortality and compensatory natality in relation to available winter food and their population size, and predation seemed a nonessential adjunct. Prior to 1967, elk (*Cervus elaphus*), bison (*Bison bison*), and prong-

horn (*Antilocapra americana*) were reduced by park staff (Craighead et al. 1972, Meagher 1973, Houston 1982, Coughenour and Singer 1991). Elk numbers were reduced to below 5,000 by 1967, and after cessation of artificial controls in 1969, elk increased dramatically (Houston 1982, Merrill and Boyce 1991). Harvests of the northern Yellowstone elk that migrated north of the park averaged only 9% of the herd during the years 1967–88 (Houston 1982, Singer 1991), a level insufficient to control the herd’s growth.

Yellowstone’s ungulate management since 1967 can not be regarded as a scientific experiment in that there is no ecosystem replication, no control situation(s) with similar climate where wolves exist, where ungulate migrations are uninfluenced by human activities, and where natural fire is unregulated (Cayot et al. 1979, Peek 1980, Kay 1987). Yellowstone National Park’s climate is different this century than last—summer temperatures are increasing and January–June

¹Current address: National Biological Service and Natural Resources Ecology Lab, Colorado State University, Fort Collins, CO 80523

precipitation levels are decreasing (Balling et al. 1992). The climatic changes might alter vegetation-ungulate relations. Evaluations of the park's management program have been limited mostly to monitoring of range plots (mostly 1958 to present), comparisons inside and outside of ungulate exclosures, and comparisons of current photos to those taken 100-120 years ago (Houston 1982, Houston and Meagher in prep.); inferences from these kinds of monitoring studies are limited (Platt 1964). Few precise criteria for testing hypotheses were provided during the original statement's of the ungulate management experiment (Houston 1976, 1982; Cole 1971), overgrazing was not defined, and equilibrium theories prevalent for the time, which have since been questioned (DeAngelis and Waterhouse 1987), were central to the original experiment (Coughenour and Singer 1991).

Houston (1982:125) who used Parker transect and chart quadrats for his analysis 1957-74, concluded there were "... little or no consistent differences between the treatments of nongrazing and grazing by native ungulates on plant species abundance, basal area, or composition. Differences over time appeared to be related more to fluctuations in growing conditions." Comparative photos from the 1970s compared to historic photos from the 1860-80s suggested no increase in gross evidence of erosion such as in visible erosive rills, exposed tree roots, or bare ground (Houston 1982). Houston (1982) concluded the effects of elk on vegetation did not exceed those expected from a population near ecological carrying capacity; fluctuations in abundance of perennial grasses were influenced more by fluctuating growing conditions, especially rainfall, than ungulate densities.

Several serious questions were raised, however, concerning ungulate densities on the northern Yellowstone winter range following Houston's (1982) study which ended in 1979. Elk counts increased to 16,000 in 1982 and then to 19,000 in 1988 (Singer 1991), raising concerns for overgrazing of the winter range (Chase 1986, Kay 1987). Bison counts also increased 154%, mule deer (*Odocoileus hemionus*) 126%, and pronghorn 215% on the northern Yellowstone winter range during the 1980s (Meagher 1989, Singer 1991), contributing to the concerns. Alternatively, the winter range might not be overgrazed. Useable elk winter range may have increased during mild

winters of the 1980s (seven of the 8 winters between 1980 and 1988 received less than the average amount of snowfall), ungulates ranged over a wider area, forage was more accessible because of the shallower snows, and elk more regularly migrated north of the park boundary beginning at about 1980, thus effectively adding 18% to their area of winter use and dispersing grazing pressures (Singer 1991).

To resolve the controversy, in 1987 the U.S. Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing (Congressional Record - Senate S.12613, 1986)."

Studies published from this large research initiative, 1986-88 did not document overgrazing of grasslands by native ungulates. Parker transect data sampled in and out of exclosures 1962-89 suggested vegetation responses to climate were much more significant than changes due to exclosure from grazing. Grasses increased in frequency of abundance until 1986 (in spite of increasing elk numbers) and forbs decreased, reverse trends were observed after 1986, apparently in response to drier conditions (Coughenour et al. 1995). Changes in plant frequency were parallel inside and outside of the ungulate exclosures. Coughenour et al. (1995) concluded elk grazing has not degraded the herbaceous vegetation of the northern winter range, but the authors pointed out problems with the sampling including: no correlation of Parker hits to plant biomass, high variances, and small sample sizes. Coughenour (1991) reported grass and forb biomass production inside and outside of exclosures was largely uninfluenced by elk grazing in 1987, but both were reduced on grazed sites in 1988, a dry year. Root biomass and soil moisture were not affected by grazing. Coughenour's (1991) sampling, however, was restricted to plant groupings; he did not separate herbaceous biomass to the species level.

The purpose of this investigation was to evaluate differences in aboveground biomass production by plant species between grazed and ungrazed sites on Yellowstone's northern elk winter range.

Methods and Study Area

The Yellowstone northern winter range consists of about 100,000 ha, of which about 82% lies within Yellowstone National Park and 18% lies north of the park on Gallatin National Forest and private lands. The Yellowstone northern winter

range is lower (1,500 m-2,400 m), warmer, and receives less precipitation than the higher plateaus of the park. Total precipitation averages less than 75 cm for most of the northern winter range. Mean annual precipitation at the lower elevations (1,620 m) at the park boundary near Gardiner, Montana, is 30 cm, but precipitation is 55 cm at 2,000 m near the Lamar Ranger Station.

The majority of the winter range is undisturbed by human activities with two major exceptions:

- (1) The 4,900 ha Boundary Line Area described by Houston (1982) was subjected to a livestock grazing, irrigation and haying of meadows and swales, and the introduction of a variety of exotic hay meadow plants (timothy, *Phleum pratense*; Kentucky bluegrass, *Poa pratensis*; smooth brome, *Bromus inermis*; quackgrass, *Agropyron repens*; cheatgrass, *Bromus tectorum*). Houston (1982) felt that prior to the agricultural activities the Boundary Line Area was dominated by needle-and-thread grass (*Stipa comata*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). I studied swales and the intervening rolling grasslands in this area, near the two Gardner ungulate enclosures.
- (2) Bison were largely restricted in the park to the Lamar Valley from about 1904-52, when bison were fed hay cut from both the native meadows, and from irrigated, cultivated fields of exotic grasses (Meagher 1973, Houston 1982). Exotic grasses that still persist in the Lamar Valley area include smooth brome, timothy, Kentucky bluegrass, and quackgrass.

About 41% of the northern winter range is forested, largely with Douglas-fir (*Pseudotsuga menziesii*) stands and a grass understory (Houston 1982, Despain 1991). About 55% of the area is grassland, especially Idaho fescue (*Festuca idahoensis*) and big sagebrush (*Artemisia tridentata*) habitat types (Mueggler and Stewart 1980), about 2% is aspen (*Populus tremuloides*) stands, and about 0.4% is willow (*Salix spp.*) and riparian shrub stands. My investigation focused on two plant community types used mostly by elk: (1) upland bunchgrass communities (ridge and slope) never subjected to agricultural activities, and (2) lower elevation, swale winter range sites grazed mostly by elk, but subjected to cattle

grazing and haying activities until 1932 on the Boundary Line Area (since my study, these swales are also being grazed by the park's expanding bison population (Meagher 1989).

Upland Bunchgrass Communities Never Disturbed by Haying Activities

Sampling was conducted within upland bunchgrass communities both inside (ungrazed) and immediately adjacent (grazed) to 82-ha enclosures for ungulates. The enclosures were erected in 1957 and 1962 between Gardiner and the Lamar Ranger Station. All 8 enclosures are on dry, upland ridges or slopes within a complex of gently rolling swales and ridges. These ridges and slopes are windblown and receive high use by elk, especially in late winter (Houston 1982). The ridges and slopes at the Gardiner enclosures were grazed by livestock until 1932, but were not subjected to the seeding or haying of grasses—no soil disturbances occurred on these sites.

Measurements in bunchgrass communities in 1986 and 1987 included biomass and cover in 10 pairs of 10x10 m macroplots (grazed and ungrazed) located with similar slope, aspect, and soil characteristics at each enclosure site. Sampling of paired plots was conducted simultaneously. Lane (1991) described the soils at the macroplot sites as Typic Calciborolls, Aridic Haploborolls, and Aridic Calciborolls. Lane (1991) found no consistent trends in soil organic matter, nitrogen, sulfur, electrical conductivity, iron, and zinc between grazed and ungrazed plots. Slopes between paired sites varied less than 6%, and aspects varied less than 18%. Ten 1x1 m quadrats or 15 0.25x0.25 m quadrats were located randomly within each larger (10x10 m) macroplot. Percent cover of each plant species, along with cover of dead litter, dung, bare ground, rocks (>6 m diameter), pebble (<6 m diameter), and pavement was estimated with a grid frame placed on the quadrats. Percent cover by dead bunchgrass clumps was estimated from the grid frame. All herbaceous and subshrub above-ground biomass was then clipped and frozen, later sorted into green and dead material by species, oven-dried for 48 hours at 60°C and weighed.

Swale Communities Subjected to Haying Activities

Swale communities in the Boundary Line Area were studied inside and outside of the two Gardiner

exclosures, but sampling was restricted to measurements of percent plant cover only. I selected 5 paired macroplots (10 m x 10 m) located inside and outside of each exclosure in swales. Each swale site was separated from the other by rolling ridges and slopes (n=10 paired macroplots total). Since these swales were small in size (about 0.1 ha) and since they were separated spatially by intervening rolling steppe vegetation, I treated each swale as an independent replicate sample, but I pooled the data within each swale. A single mean value from all the plots in each swale was used in a 1-way ANOVA with grazing as the treatment and individual swales as replicates. Physical evidence (farm machinery parts, ditches) indicated these swales were seeded and grazed by livestock, and some were irrigated prior to 1934. These swales were likely mechanically seeded, but were probably not plowed under.

Nutritional and fibrous constituents were sampled after senescence in August at 2 of the eight total exclosures. The two exclosures sampled were located on the Blacktail Deer Creek. Crude protein, fat fiber, Van Soest fibers, total ash, gross energy, in vitro digestibility (IVDDM, Tilley and Terry), and Calcium, Phosphorus, Manganese, Potassium, and Magnesium levels were determined (Wildlife Management Habitat Lab, Pullman) for the three most common forage grasses, bluebunch wheatgrass, junegrass (*Koeleria pyramidata*), and Idaho fescue. Heights and numbers of reproductive culms and vegetative leaves were counted and measured for the same three grasses on a 20 cm x 30 cm subplot within each quadrat.

Each exclosure represented one replicate (Hurlbert 1984) of the grazing treatment (grazed vs. ungrazed). One mean value for each exclosure was compared for only the most common species and plant categories (forb, subshrub, total grasses) that were present at all locations with 1-way ANOVA. Percent ground cover categories were compared between grazed and ungrazed sites, with the non-parametric Kruskal-Wallis test. The data was not transformed because of the large number of small and zero values of cover categories and biomass.

Grass morphology and reproductive characteristics were compared with Mann-Whitney U tests because the data were not normal (Kolmogorov-Smirnov test), and the variances were heteroscedastic (F-max test, Sokal and Rohlf 1969). Nutritional and fibrous constituents were

compared between grazed and ungrazed sites with the t-test.

Results

Most of the ungulate herbivory near the eight exclosures was attributed to elk, with some herbivory by bison. Herbivory by pronghorn and mule deer occurs at the Boundary Line Area near the Gardiner exclosures, but these ungulates are primarily browsers in the study area (Singer and Norland 1995). Elk outnumber other ungulates on the northern Yellowstone winter range by ratios of 100 elk:14 mule deer:3 bison:2 pronghorn:2 bighorn sheep (*Ovis canadensis*):1 moose (*Alces alces*) (Singer 1991). Bighorns and moose were not observed near the exclosures. Rodents (*Lepus townsendi*, *L. americanus*, *Spermophilus armatus*) occur near the exclosures and pass freely in and out of the fences.

Ungulate herbivory at the exclosure sites was restricted almost entirely to winter, but some grazing of early spring grass occurs just prior to elk leaving the winter ranges (Houston 1982). Spring off-take was zero near the Blacktail exclosure in 1990 (Singer and Harter unpubl. data), but spring off-take was more significant in the Lamar Valley (Frank and McNaughton 1992). Elk vacated the winter range sites during the remainder of the growing season (Houston 1982). Bison, however, recently shifted their area of winter range use westward (Meagher 1989) and began wintering near the Junction Butte in 1983, and to a limited extent near the Gardiner exclosures since 1988.

Comparisons of Herbaceous Biomass in Grazed and Ungrazed Bunchgrass Communities Not Subjected to Agricultural Activities

Less standing crop of annual green herbage biomass was collected on grazed sites than on ungrazed sites in 1986 ($F = 45.7$, $P < 0.01$, Table 1), but not in 1987 ($P > 0.05$). Forb biomass was not influenced by grazing in 1986 ($F = 2.0$, $P = 0.12$), but the difference due to grazing approached significance in 1987 ($F = 2.4$, $P = 0.10$). Less grass biomass was produced on grazed sites in 1986 ($F = 28.0$, $P < 0.01$), but not in 1987 ($P > 0.05$). Numerically, 85% less biomass of rosy pussytoes (*Antennaria microphylla*) and 33% less fringed sage (*Artemisia frigida*) was collected from grazed sites, but the differences were statistically not significant ($P > 0.05$).

TABLE 1. Comparisons of biomass between grazed and ungrazed bunchgrass communities on Yellowstone's northern elk winter range.

	1986 (n = 4 macroplots)						1987 (n = 6)					
	Ungrazed			Grazed			Ungrazed			Grazed		
	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE
Bluebunch Wheatgrass	13.4		6.6	8.3		2.9	7.6		2.8	7.6		2.8
Idaho Fescue	8.3		2.9	5.9		2.7	7.2		1.6	10.0		2.0
Junegrass	7.3		2.5	4.7		1.4	4.8		1.6	10.0		2.0*
Total Grasses	49.8		4.7	18.9		1.9**	24.4		5.6	31.6		5.2
Total Sedges	0.2		0.1	0.4		0.1	0.4		0.3	0.4		0.2
Rosy Pussy-toes	1.0		0.2	0.9		0.4	10.8		6.8	0.8		0.4
Total Forbs	22.5		6.6	10.9		2.5	26.0		8.8	10.8		3.6~
Fringed Sage	3.3		1.8	1.4		0.7	4.8		2.0	4.0		2.0
Total Shrubs and Subshrubs	3.8		2.0	2.0		1.0	10.8		1.6	6.4		2.8
Total Green Herbage Production	76.1		4.3	31.8		3.8**	62.0		11.2	49.2		6.0

** $P < 0.01$, * $P < 0.05$, ~ $P \leq 0.01$. Biomass differences were tested using 1-way ANOVA with location as replicates and grazing as the treatment.

¹Does not include biomass of the perennial succulents, *Opuntia spp.*, which occurred at the lowest elevation, Gardiner exclosures, because I could not differentiate annual from perennial growth. *Opuntia spp.* biomass (annual plus perennial) was 19.2 ± 9.64 g/m² on protected sites and 9.6 ± 7.4 g/m² on grazed sites.

Several other plant species were less ubiquitous in the study plots, and inferences concerning grazing treatment effects are tenuous. For example, thick-spiked wheatgrass (*A. dasystachum*) was found at only the two highest exclosure locations in the Lamar Valley where it was more abundant on grazed (6.2 ± 0.9 g/m²) than on ungrazed sites (3.5 ± 0.7 g/m²) ($P < 0.05$).

Elk herbivory did not influence the frequency of grass, forb or shrub species (Table 2, $P > 0.05$). An average of 4.5 grass species, 17.5 forb species and 3.5 shrub species were identified on each 10 m x 10 m macroplot in bunchgrass communities. One species, *Arabis holboellii*, was recorded from only grazed plots.

Lichen cover was not influenced by elk herbivory ($P > 0.05$, Table 3), but moss cover was significantly greater on ungrazed sites in 1986 ($P < 0.05$), but not in 1987 ($P > 0.05$). Litter and standing dead vegetation averaged 3.5 times more biomass on ungrazed plots ($P < 0.05$, Table 3), and as a result bare ground averaged 3.8 times more on grazed sites both years (Table 3). Pebble cover, however, averaged 50% less on grazed sites ($P < 0.05$), probably because pebbles were less obvious on grazed areas due to hoof action and soil compaction by ungulates. When bare ground and pebble cover were combined, all bare surfaces averaged only 18% more on grazed versus

ungrazed sites in 1987 ($P < 0.05$), but the difference was not significant in 1986 ($P > 0.05$, Table 3). Small pebble cover was greater on ungrazed plots both years. Animal dung from ungulates and rabbits provided a minor amount of ground cover (1.2-4.1%) and its abundance was greater on grazed than ungrazed sites ($P < 0.05$) (Table 3).

I observed no evidence of any significant increase in bunchgrass mortality due to elk herbivory ($P > 0.05$, t-test, $t = 0.54$). Dead bunchgrass clumps averaged 4.3% cover for both treatments.

Grass Morphology

Numbers and heights of reproductive culms and numbers of vegetative culms did not vary between grazed and ungrazed paired plots for bluebunch wheatgrass, Idaho fescue, junegrass, thick-spiked wheatgrass, needle-and-thread grass (*Stipa comata*), or bluegrasses (Table 4). The single exception was more vegetative culms of junegrass were sampled per individual plant on grazed sites. Heights of vegetative leaves were shorter in grazed sites of bluebunch wheatgrass ($t = 5.7$, $P < 0.001$), Idaho fescue, junegrass, thick-spiked wheatgrass, and bluegrasses ($P < 0.05$). Reproductive ratio (the number of reproductive vs. the number of vegetative culms per plant) did not vary between grazed and ungrazed paired plots for any grass species ($P > 0.05$).

TABLE 2. Number of grass, forb, and shrub species compared between 10 pairs of grazed and ungrazed macroplots, in 1986 and 1987 from upland bunchgrass communities on Yellowstone's northern range.

No. Plant Species	1986							
	Mammoth-W		Mammoth-E		Blacktail-W		Blacktail-E	
	Control	Grazed	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	6	4	4	5	4	4	6	3
No. Forbs	8	7	15	10	26	25	16	21
No. Shrubs	5	3	3	5	2	3	2	2
TOTAL	19	14	22	20	32	32	24	26

No. Plant Species	1987					
	Gardiner-E		Gardiner-W		Blacktail	
	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	2	2	4	3	4	4
No. Forbs	11	16	21	17	10	12
No. Shrubs	0	1	3	2	2	3
TOTAL	13	19	28	22	16	19

No. Plant Species	Junction Butte		Lamar-E		Lamar-W	
	Control	Grazed	Control	Grazed	Control	Grazed
	Control	Grazed	Control	Grazed	Control	Grazed
No. Grasses	3	8	5	5	3	4
No. Forbs	19	17	22	21	27	32
No. Shrubs	2	2	1	1	3	3
TOTAL	24	25	28	27	33	39

TABLE 3. Ground cover categories and standing dead and downed litter on grazed and protected bunchgrass communities in Yellowstone National Park, 1986-87. Differences were tested using the Kruskal-Wallis 1-way ANOVA with grazing as treatment and locations (n = 4 or 6) as replicates.

	1986 (n = 4)						1987 (n = 6)					
	Ungrazed			Grazed			Ungrazed			Grazed		
	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE	$\bar{x}$	$\pm$	SE
Lichen Cover(%)	6.3		3.3	9.8		8.0	4.2		1.1	5.1		3.9
Moss Cover (%)	10.4		3.9	1.7		0.2*	1.9		0.4	0.6		0.3
Bare Ground (%)	11.7		5.1	20.2		2.5*	4.4		0.3	35.1		6.5*
Pebble Cover ¹ (%)	29.4		4.5	18.3		8.9	37.0		8.2	13.8		0.7**
All Bare Surfaces ² (%)	41.1		5.1	38.5		2.5	41.4		4.1	48.8		2.7*
Animal Dung ³ (%)	0.2		0.1	34.3		11.6**	1.2		0.3	4.1		1.2*
Litter and Standing Dead												
Vegetation (g/m ²)	84.4		16.4	21.1		7.2**	67.0		9.3	23.3		3.9**
Dead Wood ⁴ (g/m ²)	2.1		0.6	1.7		0.5	3.2		0.7	2.0		0.7

¹Pebbles were defined as < 6cm diameter.

²Bare ground and pebble cover combined.

³Elk, pronghorn, deer and rabbits pellets as percent of ground cover in 1987, and total number of pellets per m² in 1986.

⁴Dead stems of shrubs (big sagebrush, horsebrush, rabbitbrush) and subshrubs (fringed sage, Phlox) lying on the ground surface.

TABLE 4. Mean morphological measurements for 3 common grasses at 8 grazing exclosures on Yellowstone's Northern Winter Range (n= 130 grazed and 130 ungrazed plots, 1-m²).

	Bluebunch Wheatgrass		Idaho Fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
No. Vegetative Culms	15.4±13.3	18.6±15.8	94.0±50.1	127.6±107.2	23.1±17.9	44.7±21.4*
No. Reproductive Culms	2.0±1.7	2.3±2.1	4.2±3.3	3.2±2.9	2.5±2.6	3.2±2.7
Tallest Vegetative Culm (cm)	22.3±2.5	18.0±1.6*	15.4±3.1	7.8±0.4*	10.1±2.3	7.6±1.0*
Tallest Reproductive Culm (cm)	27.1±13.7	29.5±11.6	33.2±9.6	24.4±9.7	18.5±10.1	13.9±7.8

* Significant difference, $p < 0.05$, Mann-Whitney U tests.

Nutritional Responses of Grasses to Grazing

Elk herbivory enhanced the protein content of live grasses. Protein content averaged 16% higher on grazed versus ungrazed paired plots for bluebunch wheatgrass ($t = 9.8$, $P < 0.0001$), 36% higher for grazed Idaho fescue ($t = 11.8$, $P < 0.001$), and 10% higher for grazed junegrass ($t = 6.8$, $P < 0.05$, Table 5). Grazing did not significantly influence digestibility (IVDDM) or fibers (NDF, ADF, ADL, $P > 0.05$). Ash content was significantly higher in grazed Idaho fescue and junegrass ($P < 0.05$, Table 5).

Grazing resulted in a minor enhancement of macronutrients. Calcium levels were higher in grazed than ungrazed Idaho fescue (0.56 ± 0.07 ppm vs. 0.41 ± 0.06 ppm, $t = 15.8$, $P < 0.001$, d.f. = 18) as were Phosphorous levels (0.16 ± 0.01 ppm vs. 0.14 ± 0.04 ppm, $t = 6.20$, $P < 0.01$) and Magnesium levels (0.14 ± 0.01 ppm vs. 0.09 ± 0.01 ppm, $t = 15.8$, $P < 0.001$). Potassium levels were higher in grazed bluebunch wheatgrass (1.14 ± 0.10 ppm vs. 0.99 ± 0.03 ppm, $t = 7.9$, $P < 0.001$). No other differences attributable to elk herbivory were observed for 5 elements (Phosphorus, Calcium, Magnesium, Potassium, Manganese) in Idaho fescue or bluebunch wheatgrass, and no differences in any elements were observed in junegrass.

Effects of Native Ungulate Grazing in the Former Agricultural Zone

Bunchgrass Communities Formerly Grazed by Livestock. Vegetation on elk grazed and ungrazed rolling bunchgrass-dominated ridges and slopes in the Boundary Line Area was similar; apparently both treatments recovered in a parallel fashion from livestock grazing terminated 54 years be-

fore. No exotic plants were sampled on either treatment and no biomass differences by plant species occurred with the single exception that more biomass of *Phlox hoodii* was sampled on sites ungrazed by elk ($P < 0.05$).

Swales Formerly Hayed and Grazed by Livestock. Swale communities in the Boundary Line Area, however, where seeding and limited soil disturbance from agriculture occurred, differed on sites grazed by native ungulates during the 54 recovery period versus those sites ungrazed by native ungulates. The differences did not suggest decreased productivity on the elk grazed sites, in fact, grass cover was nearly double and bare ground less on the elk grazed sites (Table 6, $P < 0.05$). Three grasses (green needlegrass; Kentucky bluegrass; Canadian bluegrass, *Poa compressa*) were more abundant on elk grazed sites ($P < 0.05$, $F = 5.7, 5.1, 3.6$, respectively), but one of these grasses is an exotic (Kentucky bluegrass) suggesting elk grazing promoted continued dominance of the sites by an exotic grass. Field pennycress (*Thlaspi arvensis*), an exotic forb, however, was more abundant on sites ungrazed by elk ($F = 3.9$, $P < 0.05$).

Discussion

Grass biomass on upland bunchgrass types was reduced in 1986 by grazing, but there was no effect from grazing in 1987. The winter of 1985-86 which preceded the 1986 growing season was characterized by an early spring snowmelt and less than normal spring precipitation (83% of average). Grazing effects on grasslands may be exacerbated during dry conditions (Coughenour 1991, Frank and McNaughton 1993) and recovery from a drought is slower on heavily-grazed sites (Young 1943). Growing season consumption by ungulates was negligible at the study sites

TABLE 5. Nutritional values of grazed and ungrazed (exclosed) grasses on Yellowstone's northern winter range, 1986 ($\bar{x} \pm \text{S.D.}$).

	Bluebunch Wheatgrass		Idaho Fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Protein (%)	7.74 $\pm$ 0.49	9.01 $\pm$ 0.80**	7.02 $\pm$ 0.56	9.58 $\pm$ 1.02**	7.95 $\pm$ 0.31	8.78 $\pm$ 0.75**
Digestibility (IVDMD, %)	60.98 $\pm$ 1.83	61.18 $\pm$ 2.46	60.06 $\pm$ 4.50	64.93 $\pm$ 3.08	61.74 $\pm$ 2.70	62.89 $\pm$ 3.26
Fiber (NDF, %)	68.69 $\pm$ 2.76	68.21 $\pm$ 1.09	73.15 $\pm$ 1.74	68.13 $\pm$ 3.69	69.63 $\pm$ 2.33	69.23 $\pm$ 2.93
Ash (AIA, %)	1.54 $\pm$ 0.32	1.49 $\pm$ 0.18	1.20 $\pm$ 0.36	2.15 $\pm$ 0.42**	0.78 $\pm$ 0.33	2.09 $\pm$ 0.57**

*Significant difference between grazed and ungrazed grasses, $P < 0.05$, ** $P < 0.01$, t-tests.

TABLE 6. Percent cover of common plant species in swale communities of the boundary line area (BLA) of Yellowstone's northern winter range. $n = 10$ plots of 1 m² randomly located in each of 10 swales within each treatment. Ungrazed sites were protected from grazing for 27 and 29 years. Each swale was considered 1 replicate sample and only 1 mean value from subplots in each swale ($n = 10$) was used a 1-way ANOVA with grazing as the treatment ($P < 0.05$). The BLA was grazed by domestic livestock until the 1930s and some areas were seeded with exotics for hay crops, thus exotic plants are more prevalent in this part of the winter range.

	Ungrazed		Grazed	
	$\bar{x}$	SE	$\bar{x}$	SE
Plant Species				
Grasses:				
<i>Stipa viridula</i>	0.4	0.4	5.5	2.0**
<i>Bromus tectorum</i> (exotic)	4.7	2.8	3.1	1.4
<i>Poa pratensis</i> (exotic)	17.1	6.2	43.8	9.1**
<i>Poa compressa</i>	0		4.5	3.1*
<i>Hordeum jubatum</i>	1.0	0.6	1.4	0.9
<i>Koeleria cristata</i>	2.1	0.8	2.2	1.0
<i>Agropyron spicatum</i>	0.9	0.5	0.3	0.1
Other Grasses ¹	5.2	2.8	3.8	1.8
Total Grasses	31.4	1.8	64.6	19.4
Forbs:				
<i>Thlaspi arvensi</i> (exotic)	2.9	1.2	0.9	0.6*
<i>Taraxacum</i> spp. (exotic)	1.0	0.5	0.3	0.2
Other Forbs ²	3.5	1.5	1.2	0.4
Total Forbs	7.4	3.2	2.4	1.2
Moss	5.1	2.2	0	

¹Other grasses included *P. sandbergii*, *H. punctuata*, *A. smithii*, *S. comota*, *A. cristatum*, *A. caninum*, *Elymus cinerius*, *B. inermis*, *Sitanion hystrix* in frequencies too low for analysis.

²Other forbs included low frequencies of *Polygonum*, *Eurotia*, *Alyssum gabrum*, *Tragapogon dubius*, *Chenopodium*, *Descuainia richardsonii*, *Lappula redowskii*.

in 1990 (F. Singer and M. Harter in press) and growing season consumption was suspected to be negligible most other years, since so few elk were observed near the study plots. But spring consumption by elk was not sampled in 1986 or

1987, and it may have been more significant than I suspected.

The response of individual plant species to grazing were minimal. Only 4% (5 of 133) of the plant species found on the macroplots reflected

biomass differences that might be attributed to grazing. Three species (rosy pussytoes, fringed sage, *Arabis holboellii*) might have decreased due to grazing (not statistically different, but a consistent trend), but two other species (junegrass and thickspiked wheatgrass) might have increased due to elk herbivory (statistical differences).

Smith (1960) rated junegrass as an increaser species in response to elk herbivory in the nearby Jackson Hole region of Wyoming and thickspiked wheatgrass was resistant to grazing; these observations are consistent with these Yellowstone northern range data. The lack of any consistent grazing responses in other grasses on the study plots is noteworthy since both Idaho fescue and bluebunch wheatgrass are sensitive to grazing and clipping experiments (Daubenmire 1940, Young 1943, Evanko and Peterson 1955, Pond 1960, Caldwell et al. 1981). However, most native ungulate herbivory of Yellowstone northern winter range occurred during winter when grasses are dormant and during the first 2 weeks of initial grass growth (Houston 1982). Other research suggests that winter combined with minimal spring grazing, as occurred on the study plots, might have few effects on grass production. For example, clipping of Idaho fescue and bluebunch wheatgrass after they had cured had minimal effects on future production (Mueggler 1969). Early spring grazing has minimal effects on production of many grasses and forbs (McCarthy and Price 1942, Stoddart 1946, Blaisdell and Pechanec 1949).

Total forb and subshrub biomass was not consistently influenced by elk herbivory. A few forbs and subshrubs were less abundant at some paired grazed sites (fringed sage, rosy pussytoes, phlox). Perhaps some of these sites received elk herbivory into the spring on newly growing forbs. Jameson (1963) concluded that forbs were more sensitive to grazing than were grasses, as my data indicates. Elk eat very few forbs during the winter months in Yellowstone National Park (only 3% of winter diets), apparently because of deep snows and forb desiccation (Singer and Norland 1995), but less litter and more bare ground on grazed sites may provide conditions that are more (or less) suitable to some plants' needs for seedling establishment, for example some forb species.

Grass cover was substantially greater on elk grazed swales in the BLA. These swales are more productive than bunchgrass communities (Hous-

ton 1982). High nutrient return in urine and feces, and stimulation of grass growth were likely in the more productive swale communities (Frank and McNaughton 1992, 1993). These swales were seeded to exotic hay grasses prior to inclusion in the park during the 1930's. Apparently, grazing by native ungulates, especially by elk, contributed to the persistence of exotic grasses, while complete protection from ungulates since 1958 contributed to the decline of exotic grasses. The dominance of exotic grasses on Lamar Valley study sites (Frank and McNaughton 1993) also suggests heavy grazing by native ungulates, both elk and bison, contributes to the persistence of the Eurasian grasses.

The maintenance of aboveground and belowground biomass of grasses on heavily grazed sites on Yellowstone's northern range may be due to the benefits of ungulate defecation and urination (Williams 1966, McNaughton 1979) and to the accelerated decomposition of plant material (Gusev and Guseva 1983). Furthermore, grass meristems may be activated by grazing (McNaughton 1984), and the growing season may be extended by enhanced water availability (McNaughton 1983) and by higher early season soil temperatures on grazed sites (Whitman 1971, Archer and Detling 1985). Total protection of bunchgrass winter range sites from native ungulate grazing for 24-27 years resulted in a 4-fold increase in accumulated dead litter and standing dead vegetation. Excessive accumulations of mulch may reduce grass production (Weaver and Rowland 1952, Jameson 1963) due to a cooler soil surface (Johnston et al. 1971, Whitman 1971), but the addition of litter increased production in other studies (Ellison 1960). Whatever the mechanism, we observed no difference in total standing crop biomass between grazed and ungrazed sites during the first year, but only about one-half the total standing crop biomass was produced on grazed sites versus ungrazed sites during a second, drier year. In contrast, Frank and McNaughton (1993) reported more consistent and numerically more biomass increases due to grazing (47% more aboveground primary production from grazed sites) in Yellowstone National Park. However, their study involved different years than mine (1988 and 1989) and they sampled primary production (I sampled standing crop only). Frank and McNaughton's (1992, 1993) study sites were more mesic, and more productive than mine. Five of

their 12 study sites were dominated by grazing resistant, exotic grasses (timothy, Kentucky bluegrass, and/or smooth brome). Their study sites were located on summer range, transition range, and upper elevation - winter range, nearly all of their sites were located at higher elevations with more precipitation than my study sites. The swale sites I studied were more similar to study sites of Frank and McNaughton's (1992, 1993), i.e., depositional, productive sites and the swale comparisons were more supportive of their conclusions. Apparently grasses were stimulated by grazing in swales, and the exotic grass, Kentucky bluegrass, continued to dominate sites grazed by elk following cessation of agricultural activities.

Grass heights and shapes did not differ following 28 years of protection from native ungulate herbivory, with the single exception that vegetative culms of most grasses were shorter in grazed areas. Grazing results in shorter, more prostrate forms of grasses (Jameson 1963, McNaughton 1984) and more horizontal leaf angles (Detling and Painter 1983). My study indicated no effect on the height or numbers of seed heads of grasses from winter and early spring grazing. In contrast, most clipping or grazing during the growing season reduced seed production of grasses (Jameson 1963, Mueggler 1975, Owen and Wiegart 1981, McNaughton 1983, Ruess et al. 1983). The effects of winter grazing on seed production, as occurred on the Yellowstone northern range study sites, are less significant than are the effects of grazing during the growing season.

Grazing enhanced protein content in grasses by an average of 21% on the study sites. Several macronutrient concentrations (Ca, Ph, Mg, K) averaged 13-36% higher in grazed versus ungrazed grasses. The average crude protein content on the northern winter range for 3 common cured grasses in early August was 7.6% on ungrazed sites and 9.1% on grazed sites. Mould and Robbins (1981) indicated dry-matter intake of forage by elk sharply increased when dietary protein concentration fell below 8%. Therefore, enhancement of protein content on the northern winter range from grazing thus may be critical to elk over-winter survival. Increases in foliage N concentrations of grasses in response to grazing have been reported elsewhere (Jameson 1963, Everson 1966, Chapin 1980, Detling and Painter 1983, Day and Detling 1990). Enhanced N content has been attributed

to greater proportion of younger stems after grazing which are higher in N and other nutrients (Jameson 1963, Owensby et al. 1970). Uptake rates of N are higher after clipping (Ruess et al. 1983), soil nutrient pools may be enhanced by dung and urine deposition (Williams 1966, Ruess and McNaughton 1987), and increased net mineralization rates (Holland and Detling 1990).

Compensatory growth of grazed grasses (*sensu* Belsky 1986 = any positive increase in plant growth due to herbivory) may have occurred in years of adequate precipitation on my study sites and also on Coughenour's (1991) and Frank and McNaughton's (1993) study sites. Total protein yield (biomass x % protein) produced in 1986 on grazed sites was only 50% that of ungrazed sites, but in 1987 grazed sites produced 156% of the total protein yield of ungrazed sites. Gordon (1988) observed greater biomass and a higher proportion of green grass available for red deer (*C. elaphus*) on sites grazed by cattle (*Bos taurus*) during the previous winter.

Conclusions

The upland bunchgrass sites under study on Yellowstone's northern winter range apparently were not overgrazed at the time of this investigation in 1986 and 1987, at least in terms of declines in aboveground biomass production, while only the most minor changes in species composition were observed. There were very few differences in plant species composition or numbers of plant species between grazed and ungrazed plots, and there was no evidence of accelerated mortality of bunchgrasses from elk herbivory. Protein concentrations and the concentrations of several nutrients were enhanced in grasses by elk herbivory. Very few differences were observed on the heights or growth form of grazed grasses. An increase in bare ground and a large decrease in accumulated litter and standing dead vegetation were observed on grazed sites which, combined with higher bulk densities, contributed to slightly lower soil infiltration rates on grazed sites (Lane 1991). Numerically less total forbs and shrubs were found on grazed sites, but the differences were not statistically significant. Less total grass biomass was found during 1 of 2 years on grazed sites. Limitations of the study include the small number of replicate comparisons ($n = 10$ paired macroplot comparisons) over only 2 years. Te-

dious hand sorting of all live and dead materials by species for this study was enormously labor intensive (> 1.3 person years) and limited the number of replicates. In addition, pre-exclosure differences in species abundance or microsite characteristics might have occurred, and possibly obscured real effects due to grazing. Parker transect data gathered at the time of exclosure in 1958 and 1962, however, does not suggest any consistent site differences at the time of exclosure (Houston 1982, Coughenour et al. 1995). Data from swale grassland types was limited to species cover data. Elk grazing on these more productive sites apparently resulted in stimulation of grasses (double the total herbaceous plant cover in grazed sites), but the elk herbivory also resulted in continued persistence of a grazing resistant exotic grass, Kentucky bluegrass, following cessation of agricultural activities. The work of Frank and McNaughton (1993) also suggests exotic grasses persist with intense elk and bison herbivory (45% consumption) in the Lamar Valley where haying activities persisted until 1952. Exotic grasses apparently declined more rapidly in ungrazed swales in the Boundary Line Area, but one exotic weed, field pennycress, was more abundant on ungrazed sites. National Park Service policy states that native animal populations be managed under conditions representing as near as possible natural conditions. Natural conditions include herbivory by native ungulates. At the time of this study,

Yellowstone's northern elk winter range supported 21 elk/km² during the winter months (Singer 1991), yet only minor differences were detected between grazed bunchgrass sites and paired sites protected from native ungulates for nearly three decades. I propose the minimal number of grazing effects observed on the study plots are due to the restriction of direct and indirect effects from ungulate activity (grazing, trampling, bedding, trailing) to the winter season only. During the winter, plants are in senescence, the ground is frozen and, in most situations, the ground is also snowcovered, minimizing the effects from herbivory by elk. I stress these findings apply only to the upland bunchgrass sites under study and to sites where native ungulate herbivory was restricted to the winter period only.

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Literature Cited

- Archer, S., and J.K. Detling. 1985. Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. *Oikos* 47:287-291.
- Balling, Jr., R.C., G.A. Meyer, and S.G. Wells. 1992. Climate change in Yellowstone National Park: Is the drought-related risk of wildfires increasing? *Climate Change* 22:35-45.
- Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127:870-892.
- Blaisdell, J.P., and J.F. Pechanec. 1949. Effect of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. *Ecology* 30:298-305.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurea. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14-24.
- Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* 51:53-72.
- _____. 1976. Wildlife management and the dynamics of ungulate populations, pp. 183-246. In: T.H. Croaker (ed), *Applied Biology* Vol. 1. Academic Press, New York.
- _____. 1979. What is this thing called carrying capacity?, pp. 2-8. In: M.S. Boyce and L. D. Hayden-Wing (eds), *North American elk: ecology, behavior and management*. University of Wyoming, Laramie.
- Cayot, L.J., J. Prukop, and D.R. Smith. 1979. Zootic climax vegetation and natural regulation. *Wildl. Soc. Bull.* 7:162-169.
- Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11:223-260.
- Chase, A. 1986. *Playing God in Yellowstone*. Atlantic Monthly Press, New York, NY. 446 pp.
- Cole, G.F. 1971. An ecological rationale for the natural or artificial regulation of native ungulates in parks. *Trans. N. Am. Wildl. Conf.* 36:417-425.
- Congressional Record. 1986. Senate hearings. S12612. U.S. House of Representatives.
- Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe in Yellowstone's northern winter range. *J. Appl. Ecol.* 28:71-82.

- Coughenour, M.B., and F.J. Singer. 1991. The concept of overgrazing and its application to Yellowstone's northern range. Pages 209-230 in: M.S. Boyce and R. Keiter (eds), Examining the Greater Yellowstone, Yale Univ. Press.
- Coughenour, F.J. Singer and J. Reardon. 1995. Parker transects revisited. In: D. Despain and R. Hamre (eds.), Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem. U.S. National Park Service, Trans. and Proc. Ser. (in press).
- Craighead, J.J., G. Atwell, and B.W. O'Gara. 1972. Elk migrations in and near Yellowstone National Park. Wildl. Monogr. 29:1-48.
- Daubenmire, R. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of southeastern Washington. Ecology 21:55-64.
- DeAngelis, D.L., and J.C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. Ecol. Monogr. 57:1-21.
- Despain, D. 1991. Yellowstone vegetation: consequences of environmental and history in a natural setting. Roberts Rinehart Publ., Boulder, CO. 239 pp.
- Detling, J.K., and E.L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 57:65-71.
- Day, T.A., and J.K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180-188.
- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot. Rev. 26:1-78.
- Evanko, A.B., and R.A. Peterson. 1955. Comparisons of protected and grazed mountain rangelands in southwestern Montana. Ecology 36:71-82.
- Everson, A.C. 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*A. smithii*). Agron. J. 58:33-35.
- Frank, D.A., and S.J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043-2058.
- Frank, D.A. and S.J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157-161.
- Gordon, I.J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. J. Appl. Ecol. 25:1-10.
- Gusev, A.A., and N.A. Guseva. 1983. Participation of wild ungulates in the decomposition of vegetation in forest-steppe ecosystems. Ekologiya 6:51-55. (Translated into English)
- Holland, E.A. and J.K. Detling. 1990. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.
- Houston, D.B. 1976. Research on ungulates in northern Yellowstone National Park. pp. 11-27. In: Research in the parks. Trans. Natl. Park Centennial Symp., Natl. Park Serv. Symp. Ser. No. 1.
- _____. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publ. Co., Inc., New York.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:184-211.
- Jameson, D. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.
- Johnston, A., J.E. Dormaar, and S. Smoliak. 1971. Long-term grazing effects on fescue grassland soils. J. Range Manage. 24:185-188.
- Kay, C.E. 1987. Too many elk in Yellowstone - book review. Western Wildlands 13:39-44.
- Lane, J. 1991. Characterization and comparisons of soils inside and outside of grazing exclosures on Yellowstone National Park's Northern Winter Range. M.S. Thesis, Mont. State Univ., Bozeman, MT.
- McCarthy, E.C., and R. Price. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. USDA, Tech. Bull. 818. 51 pp.
- McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113:691-703.
- _____. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.
- _____. 1984. Grazing lawns: animals in herds, plant form and coevolution. Am. Nat. 124:863-886.
- Meagher, M. 1973. The bison of Yellowstone National Park. Natl. Park Serv. Sci. Monogr. 1:1-161.
- _____. 1989. Range expansion by bison of Yellowstone National Park. J. Mammal. 70:670-675.
- Merrill, E.H., and M.S. Boyce. 1991. Summer range and elk population dynamics. Pages 263-273 in: R.A. Keiter and M.S. boyce, eds. The Greater Yellowstone Ecosystem: Redefining America's Wild Heritage. Yale Univ. Press, New Haven.
- Mould, E.D., and C.T. Robbins. 1981. Digestive capabilities of elk compared to white-tailed deer. J. Wildl. Manage. 46:22-29.
- Mueggler, W.F. 1969. Responses of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48:942-949.
- _____. 1975. Rate and pattern of vigor recovery in Idaho Fescue and bluebunch wheatgrass. J. Range Manage. 28:198-204.
- Mueggler, W.F., and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Gen. Tech. Report INT-66. 154 pp.
- Owen, D.F., and R.G. Wiegert. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. Oikos 36:376-378.
- Owensby, C.E., R.M. Hyde, and K. Anderson. 1970. Effects of clipping and supplemental N and water on loamy upland bluestem range. J. Range Manage. 23:341-346.
- Peek, J.M. 1980. Natural regulation of ungulates. Wildl. Soc. Bull. 8:217-227.
- Platt, J.R. 1964. Strong inference. Science 16:347-353.
- Pond, F.W. 1960. Vigor of Idaho fescue in relation to different grazing intensities. J. Range Manage. 13:28-30.
- Rohlf, F.J., and R.R. Sokal. 1969. Statistical tables. W. H. Freeman and Co., Publ., San Francisco. 253 pp.
- Ruess, R.W., S.J. McNaughton, and M.B. Coughenour. 1983. The effects of clipping, nitrogen source, and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. Oecologia 59:253-261.
- Ruess, R.W., and S.J. McNaughton. 1987. Grazing and the dynamics of nutrients and energy regulated microbial processes in the Serengeti grasslands. Oikos 49:101-110.

- Sinclair, A.R.E. 1977. The African buffalo—a study of resource limitation of populations. Univ. of Chicago Press, Chicago.
- Singer, F.J. 1991. The ungulate prey base for large predators in Yellowstone National Park. Pages 323-348. In M.S. Boyce and R. Keiter, eds. Examining the Greater Yellowstone, Proc., Laramie, Wyo. Yale Univ. Press, New Haven.
- Singer, F.J. and J.E. Norland. 1994. Niche relationships within a guild of ungulates following release from artificial controls, Yellowstone National Park, Wyoming. Can. J. Zool. 72:1383-1394.
- Singer, F.J. and M.K. Hauter. 1995. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecol. Applic. (in press).
- Stoddart, L.A. 1946. Some physical and chemical responses of *Agropyron spicatum* to herbage removal at various seasons. Utah Agr. Exp. Sta., Bull. 324. 24 pp.
- Weaver, J.E., and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield and structure of native grassland. Bot. Gaz. 114:1-19.
- Whitman, W.C. 1971. Influence of grazing on microclimate of mixed grass prairie, pp. 207-218 in K.M. Kreitlow and L. Hart, eds. Plant Morphogenesis as a Basis for Scientific Management of Range Resources. USDA Agric. Res. Serv. Misc. Publ. No. 1271.
- Williams, C.H. 1966. Nitrogen, sulfur and phosphorus, their interactions and availability. Trans. Internatl. Soil Sci. Soc. (Aberdeen, Scotland) 1966:93-111.
- Young, V.A. 1943. Changes in vegetation and soil of Palouse prairie caused by overgrazing. J. For. 41:834-838.

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Distribution and Habitat of the Western Gray Squirrel (*Sciurus griseus*) on Ft. Lewis, Washington.

Abstract

Sciurus griseus has been accorded a "threatened" status by the Washington Department of Wildlife. Our objectives were to determine the distribution, abundance, and factors limiting the abundance of *Sciurus griseus* on Fort Lewis. Between June 1992 and August 1993 we conducted walking surveys for squirrels in 169 oak-conifer stands (approximately 700 ha). We observed 38 individual squirrels in 30 of the stands. We compared occupancy of oak stands by size, distance to water, and vegetation characteristics. We found that oak stands used by squirrels generally were: 1) > 2.0 ha, 2) < 0.6 km from water (lake, marsh, stream, or river), 3) on average, 34% *Quercus garryana*, 53% *Pseudotsuga menziesii*, and 13% other tree species, and 4) diverse in food-producing trees and shrubs including *Acer macrophyllum*, *Fraxinus latifolia*, and *Oemleria cerasiformis*. *Sciurus griseus* is associated with *Quercus garryana* woodlands which are dwindling due to human development. Fort Lewis holds the largest publicly-managed area of *Quercus garryana* in the Puget Sound region. In order to protect *Sciurus griseus* populations we recommend: 1) informing the public about *Sciurus griseus* and its status to reduce squirrel deaths by automobiles and 2) conserving and actively managing oak woodlands.

Introduction

Western gray squirrels (*Sciurus griseus*) are found in Washington, Oregon, California, and Nevada (Carraway and Vertz 1994). The State of Washington lists the western gray squirrel as "threatened" (Washington Department of Wildlife 1993). The western gray squirrel was once commonly seen in Oregon white oak (*Quercus garryana*) woodlands bordering prairies in river valleys in the Northwest (Bowles 1921). But these oak woodlands are being replaced by conifers, agricultural lands, and human dwellings and the squirrel exists in small, scattered populations in Washington.

Western gray squirrels inhabit three areas in Washington: Klickitat County along the southern Columbia River and its tributaries; in Okanogan and Chelan Counties in the northern Columbia River basin; and in the Puget Trough, in particular, Fort Lewis Military Reservation (Rodrick 1987; Figure 1). Because the U. S. Department of Defense gives special consideration in its land management to sensitive species, we studied the population on Fort Lewis. The objectives of our study were to describe the distribution, abundance, habitat, behavior, and factors possibly limiting abundance of western gray squirrels on Fort Lewis.

Study Area

Fort Lewis lies in the Puget Trough between Olympia and Tacoma, in Thurston and Pierce Counties, Washington. It consists of approximately 34,400 ha of forests, prairies, wetlands, and developed areas, including 1,200 ha of Oregon white oak woodlands. Fort Lewis maps show > 400 distinct oak woodlands ranging in size from < 0.2 ha to > 44 ha (Figure 2). Oak woodlands are most commonly found adjacent to prairies, ponds, lakes, and marshes, and at the top or bottom of hills.

Methods

Distribution and Abundance

We used maps of oak woodlands and reports of historical sightings of western gray squirrels to begin our study. First we tried to live trap squirrels, then we used walking surveys, to determine the distribution of squirrels.

Trapping. We located 10 areas on Fort Lewis where squirrels had been seen and set traps in them for a total of 4,162 trap nights from April 21 to September 4, 1992. We used wire box traps and several types of bait: peanut butter-oat mix, tuna cat food, candy bars, dried corn, whole cracked

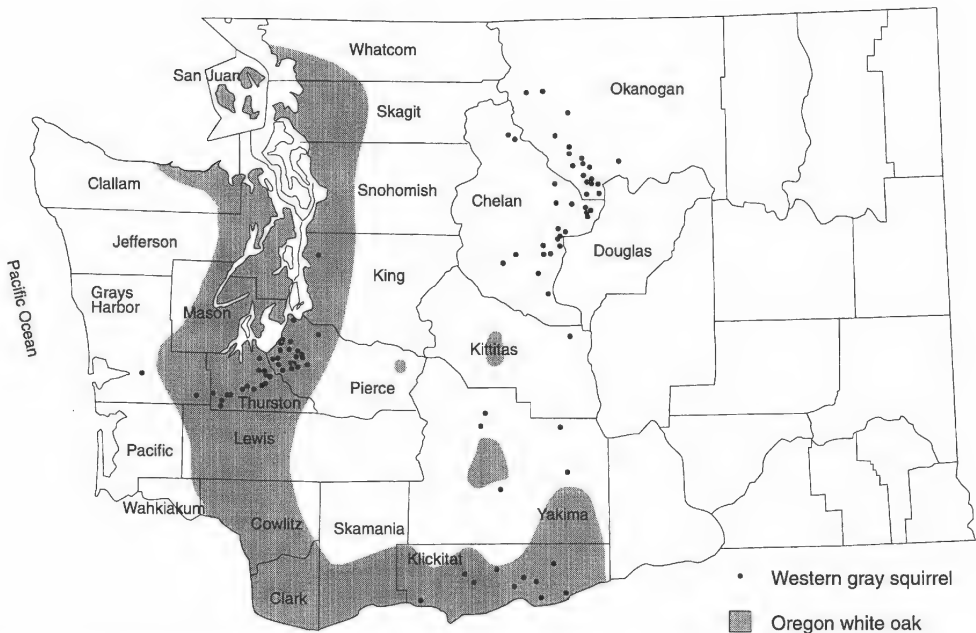


Figure 1. Distribution of *Sciurus griseus* (Rodrick 1986) and *Quercus garryana* woodlands (Stein 1990) in Washington.

walnuts, pecan halves, and peanuts in the shell. Traps were prebaited for 3 days prior to trapping. Initially, traps were placed on the ground, 30 m apart, in a grid pattern throughout the stands. After several weeks with no trapping success, we moved traps closer to the base of trees with stick nests, using no formal grid pattern. Only two squirrels were captured and we abandoned trapping as a method.

Surveys for Distribution. We conducted surveys on foot to determine the presence of western gray squirrels in 313 oak stands covering 910 ha on Fort Lewis from June 1992 to August 1993. We did not formally survey oak stands in artillery impact areas, housing areas, and developed areas because of lack of access and high human disturbance. We routinely saw eastern gray squirrels (*Sciurus carolinensis*), but not western gray squirrels, in the housing and business areas. Of the 313 stands visited, 85 were eliminated from further surveys because in our subjective evaluation they appeared unsuitable for western gray squirrels because of one or more of the following factors: 1) < 0.1 ha in size, 2) < 5 oaks, 3) within developed areas, and 4) > 500 m from adjacent

conifers. In preliminary surveys in three stands known to have squirrels, squirrels were seen during 71% of visits to each stand, on average, and were active throughout the day. We concluded that 3 visits were sufficient to determine if squirrels were present in a stand. We intensively surveyed (3 surveys) 169 stands of the 228 remaining oak stands for squirrels on three different days between 0700 and 1630. Each stand was surveyed in its entirety by observers walking through the stands at 1.0-1.5 km per hour, pausing about every 15m to listen and search for squirrels. Observers recorded the time, location, and activities of squirrels seen or heard. A sighting was considered an independent observation if it was seen > 500 m from other sightings. This distance was an arbitrary distance chosen to prevent counting the same squirrel more than once. It is unlikely that we saw all squirrels present in each stand we surveyed.

We classified the oak stands into three groups based on the number of squirrel sightings in the stand. We assumed that consistency of detection reflected consistency of use. Stands were considered high use if squirrels were seen there

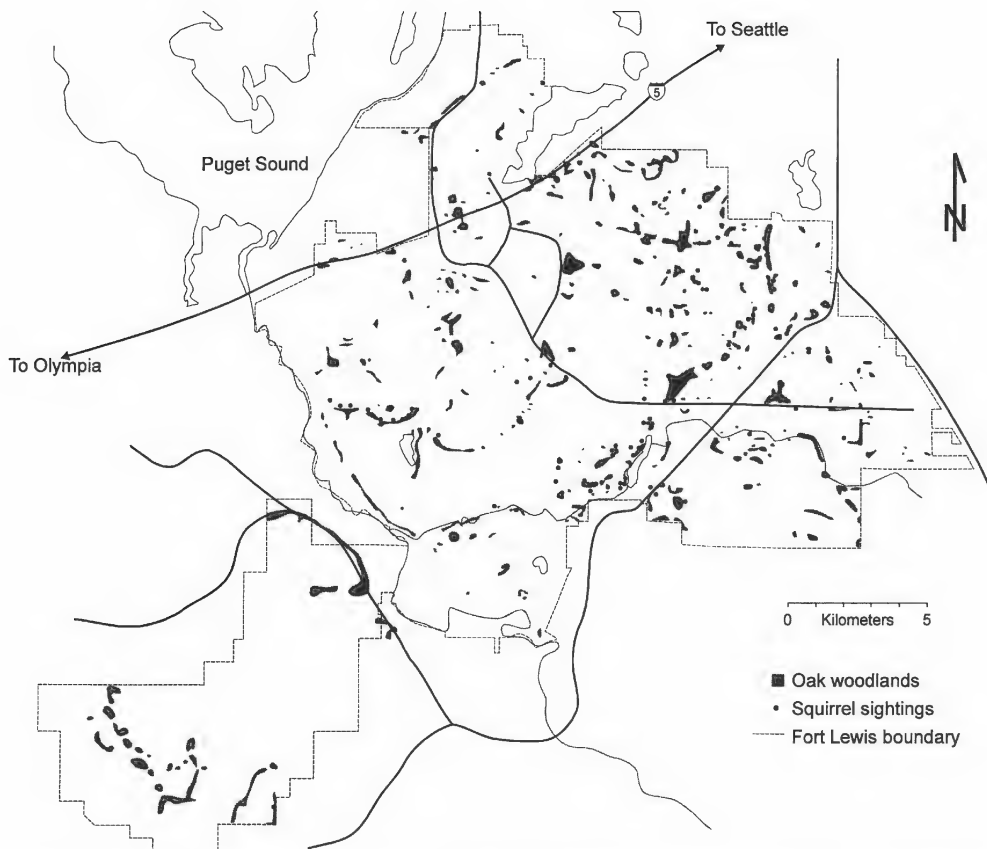


Figure 2. Locations of *Sciurus griseus* sightings (including road kills) and *Quercus garryana* woodlands (Fort Lewis Geographical Information Systems), Fort Lewis, Washington, 1992-1993.

consistently ($\geq 67\%$ of visits) or if three or more squirrels were seen on any one visit. We assumed that these stands had high use by western gray squirrels even though we rarely saw more than one squirrel per visit. Stands with one or two sightings over 3 visits were considered moderate use stands. The stands in a random sample of 26 surveyed stands in which no squirrels were seen were considered low-use. We could not assume that squirrels never used these areas. Thus, our classification relates as much to consistency of activity as to abundance or density of squirrels.

Describing Stands

For each of 30 stands in which squirrels were seen, we measured species composition, density,

and basal area of trees and species composition and percent cover of understory vegetation. We also chose a random sample of 30 stands from the 139 surveyed stands in which squirrels were not seen; but, because of heavy military activity, only 26 of these stands were actually measured. Therefore, a total of 56 stands were measured.

We used the point-centered quarter (PCQ) method of vegetation sampling for trees (Cottam and Curtis 1956). We placed PCQ points throughout the oak and oak-conifer stand in a grid pattern, 15-50 m apart, depending on the size of the stand, in order to sample 15-30 points (60-120 trees) per stand. We kept points > 15 m from the edge of the stand to avoid edge effects. We used 10-25 1.5-m-radius plots systematically spaced

throughout the stand to sample percent vegetation cover and dominant taxa for each of three life forms: 1) herbaceous: ferns, forbs, and grasses, 2) woody: shrubs and seedling and sapling trees < 4 m, and 3) understory trees > 4 m and < 10 cm diameter at breast height (DBH). We followed the taxonomy and nomenclature of Hitchcock and Cronquist (1991). We measured distance to water from squirrels and oak stands on 1:24,000 7.5 minute quadrangle maps and in the field when any unmapped water sources were found during surveys.

We calculated means for all variables measured in each stand, and then we averaged the means to determine means for each group of stands: high, moderate, and low use. As an exploratory analysis of features associated with gray squirrels, we compared the means for several variables in the three groups by using analysis of variance (ANOVA) and multiple range tests of variance (Duncan's and Student-Newman-Keuls). Although some protection from erroneous significance due to multiple comparisons is provided by the procedures supplementing the ANOVA, there is still a risk that differences appearing significant at any preferred *p* value are not. Additionally, the analysis was *post hoc* and exploratory; thus caution must be used in extrapolating our results and using them as predictors.

We classified each of the high, moderate, and low use stands by size (0.4-2.0 ha; 2.1-8.0 ha; > 8.0 ha) and distance from water (<0.1 km; 0.1-0.39 km; 0.4-0.69 km; 0.7-1.0 km; >1.0 km). To evaluate the influence of size and distance to water on use by western gray squirrels, we ran Chi-square tests on the number of stands in high, moderate, and low use groups in each size and distance class, reflecting our emphasis on consistency of use and our inability to measure abundance. This was a retrospective, exploratory analysis.

After recognizing that both the size of the stand and distance to water could be influencing the presence of western gray squirrels in a stand, we did an additional, prospective, experimental test to quantify these influences. We chose random samples of 10 stands, in each of 6 categories based on size and distance to water (a total of 60 stands). We surveyed each stand three times for squirrels and determined the number of stands in which squirrels were present. Two stands had to be recategorized following surveys because we found

additional water sources there. One of these stands was also smaller than what was shown on the original oak stand map. This created unequal sample sizes. We performed Chi-square tests to compare western gray squirrel use of stands cross-classified by size and distance to water.

Behavioral Observations

The presence of squirrels at any specific location and the length of observable activity periods was unpredictable, so we did not do time-controlled activity budgets during this study. Rather, we opportunistically recorded observations from August 1992 through August 1993. We approached oak stands with squirrels slowly and quietly, sat where we could see a large area of habitat, and recorded squirrel activities. We also recorded activities of all squirrels seen during walking and driving surveys and combined this information with data from behavioral observations to determine general seasonal behaviors. We grouped behaviors into seven categories: 1) foraging, 2) traveling, 3) resting and grooming, 4) agonistic interactions, 5) mating, 6) escaping and warning, and 7) alert and watching and determined the duration of activities for all observations. We compared proportions of time spent in each activity by season using pie charts. We compared relative time spent on the ground with time spent in trees using Chi-square tests.

Results

Distribution and Abundance

During 406 hours of surveys we saw 46 western gray squirrels, or 1 squirrel per 8.8 hours of survey time. These 46 sightings reflected at least 38 individual squirrels in 30 of the 169 stands surveyed. We intensely surveyed about 74% of the possible western gray squirrel habitat (228 stands) on Fort Lewis. We and Fort Lewis Forestry and Wildlife personnel documented 272 western gray squirrels observed outside of formal surveys from April 1992 to August 1993. When we mapped these locations, 43 individuals and 14 stands were added to the 38 individuals seen in 30 stands during surveys. Thus, approximately 81 individual western gray squirrels were seen from April 1992 to August 1993 in 44 separate oak stands. Of these 81, 13 were found dead on roads and two were found dead on the ground within an oak stand.

The cause of death of the two squirrels in the oak stands was not determined; there were no signs of injuries or predation. Most road-killed squirrels (11 of 13) were found from April to August; two were pregnant, a third was lactating, and four others were juveniles. Squirrels were seen most often in large oak-Douglas-fir stands near water (Figure 2). They were never seen in pure oak stands that were isolated from conifers and water. Eighty-four percent (267 of 318) of total western gray squirrel sightings were ≤ 390 m of a source of water. About 31% of all oak stands were ≤ 390 m from water.

Habitat Characteristics—Post Hoc Comparisons

Oak stands on Fort Lewis were highly variable in the composition and abundance of forest-floor vegetation and shrubs and the density and abundance of tree species (Table 1). Stand size varied from 0.4 ha to 48 ha, while distance to water varied from < 0.1 km to > 1.0 km. Many plant species that produce squirrel food were rare, with an average percent cover of $< 5\%$ (Table 1), but were abundant in particular stands (10–20% cover), resulting in high variability in the average number of mast species per stand.

The characteristics of oak stands in our retrospective survey differed significantly between high and low use stands in terms of size of the stand, distance from water, tree species composition, basal area of stand, and understory plant species composition at the three life form levels (Table 2). Moderate use stands had some characteristics of both high and low use stands. High-use stands were larger (Table 3) and closer to water (Table 4) than low-use stands. High-use stands had an overstory with an average of 34% oak, 53% Douglas-fir, and 13% other tree species. Low-use stands had an average of 53% oak, 43% Douglas-fir, and $< 5\%$ other tree species. The relative frequency of Oregon white oak trees was significantly greater in low-use stands than in high-use stands. There was no significant difference in the relative frequency or the average DBH of Douglas-fir trees between high- and low-use stands but high-use stands had a significantly higher average basal area of Douglas-fir (Table 2). High-use stands had a greater diversity of tree species (16 species) than low-use stands (13 species) and greater abundances of bigleaf maple (*Acer macrophyllum*), Oregon

TABLE 1. Vegetation in 56 *Quercus garryana* woodlands on Fort Lewis, Washington, 1993.

Habitat Element	Mean	CV ¹	Range
HERBACEOUS PLANTS (% cover)			
Total	39	42	9 - 83
Forb	53	48	6 - 92
Grass	33	79	0 - 93
Moss	30	95	0 - 100
Fern	25	77	0 - 81
SHRUBS (% cover)			
Total	46	29	15 - 73
<i>Cytisus scoparius</i>	19	46	0 - 100
<i>Berberis aquifolium</i>	10	90	0 - 46
<i>Holodiscus discolor</i>	7	117	0 - 33
<i>Berberis nervosa</i>	4	113	0 - 40
<i>Symphoricarpos albus</i>	48	145	0 - 100
<i>Corylus cornuta californica</i> (< 4 m)	22	169	0 - 77
<i>Oemleria cerasiformes</i>	10	128	0 - 54
<i>Pseudotsuga menziesii</i>	8	147	0 - 54
<i>Quercus garryana</i>	5	254	0 - 27
<i>Gaultheria shallon</i>	4	216	0 - 64
<i>Amelanchier alnifolia</i>	3	278	0 - 21
<i>Rosa gymnocarpa</i>	1	250	0 - 14
<i>Rubus procerus</i>	1	370	0 - 18
<i>Vaccinium ovatum</i>	1	300	0 - 20
<i>Ribes</i> sp.	1	367	0 - 13
UNDERSTORY TREES (% cover)			
Total	8	84	0 - 32
<i>Pseudotsuga menziesii</i>	9	110	0 - 33
<i>Quercus garryana</i>	7	114	0 - 39
<i>Acer macrophyllum</i>	2	238	0 - 24
<i>Corylus cornuta</i> (> 4.0 m)	2	265	0 - 23
<i>Fraxinus latifolia</i>	2	347	0 - 27
CANOPY			
Density (trees/ha)	225	158	12 - 440
% <i>Quercus garryana</i>	45	54	5 - 100
% <i>Pseudotsuga menziesii</i>	48	45	0 - 85
% Other trees	7		0 - 42
Basal area (m ² /ha)	21	46	0.8 - 44
Median DBH (cm) <i>Quercus garryana</i>	21	25	12 - 40
Median DBH (cm) <i>P. menziesii</i>	47	32	19 - 102

¹ Coefficient of variation expressed as a percent.

ash (*Fraxinus latifolia*), bitter cherry (*Prunus avium*), cascara (*Rhamnus purshiana*), and western red cedar (*Thuja plicata*) than low-use stands. Some of the differences in diversity of tree species may be due to the differences in stand sizes (i.e., a species-area effect).

There were differences in vegetation in the three life form levels between high- and low-use oak stands. High-use stands had a higher percent cover of understory trees than low-use stands. The

TABLE 2. Characteristics of *Quercus garryana* woodlands with differential use¹ by *Sciurus griseus*, Fort Lewis, Washington, 1993.

	High use		Moderate use		Low use		
Habitat feature	n=18		n=12		n=26		p-value
	Mean	(SE)	Mean	(SE)	Mean	(SE)	
# Food species ²	8.3	(0.5)	6.4	(0.5)	5.6	(0.4)	0.00
DBH ³ QUGA ⁴	21.5	(1.1)	21.7	(2.0)	25.9	(6.1)	0.51
DBH PSME	48.5	(2.1)	48.9	(6.4)	44.4	(2.7)	0.58
Trees/ha	243.8	(17.0)	216.7	(21.5)	215.3	(21.0)	0.56
% QUGA	34.1	(3.1)	43.6	(6.7)	52.5	(4.9)	0.03
% PSME	53.3	(3.3)	51.9	(6.6)	43.0	(4.9)	0.25
% other trees	12.6	(3.3)	4.5	(2.3)	4.8	(1.7)	0.03
BA ⁵ (all trees)	27.0	(2.0)	22.2	(2.6)	16.2	(1.8)	0.00
BA QUGA	4.1	(0.9)	3.9	(0.9)	3.9	(0.6)	0.97
BA PSME	29.0	(5.5)	21.7	(3.5)	14.4	(1.7)	0.02
% Ground cover	31.5	(2.8)	36.1	(5.7)	46.1	(2.9)	0.01
% Shrub cover	41.9	(1.8)	44.8	(4.1)	50.3	(3.1)	0.13

¹ High use = western gray squirrels were seen > 2 times or > 2 squirrels seen simultaneously; moderate use = squirrels seen 1 or 2 times; low use = squirrels never seen in stand.

² Food species include *Symphoricarpos albus*, *Corylus cornuta*, *Oemleria cerasiformes*, *Pseudotsuga menziesii*, *Quercus garryana*, *Gaultheria shallon*, *Amelanchier alnifolia*, *Rosa* sp., *Rubus procerus*, *Vaccinium parvifolium*, *Ribes* sp., *Acer macrophyllum*, *Acer circinatum*, *Fraxinus latifolia*, *Pinus ponderosa*, *Rhamnus purshiana*, *Taxus brevifolia*, *Abies grandis*, *Cornus nuttallii*, *Populus trichocarpa*, and *Pyrus malus*.

³ QUGA = *Quercus garryana*, PSME = *Pseudotsuga menziesii*.

⁴ DBH = diameter at breast height in centimeters.

⁵ Basal area in meters²/hectare.

TABLE 3. A retrospective comparison¹ of the percent of oak stands across 3 size classifications for three samples of oak stands; 1) 18 stands with high western gray squirrel use; 2) 12 stands with moderate use; and 3) a random sample of 26 stands in which no squirrels were seen (low use); 56 stands total; Fort Lewis, Washington, 1992-1993.

Size ³	Stand use ²		
	High	Moderate	Low
1	22	25	50
2	44	33	46
3	33	42	4

¹ Statistical results: Pearson Chisquare = 10.354; df = 4; p = 0.035.

² High use = western gray squirrels seen in stand > 2 times or > 2 squirrels seen simultaneously; moderate use = squirrels seen in stand 1 or 2 times; low use = squirrels never seen in stand.

³ Size classes: 1 = 0.4-1.9 hectares, 2 = 2.0-8.0 hectares, 3 = >8.0 hectares.

TABLE 4. A retrospective comparison¹ of the percent of stands across 5 distance-from-water classifications for 3 samples of Oregon white oak stands: 1) 18 stands with high western gray squirrel use, 2) 12 stands with moderate use, and 3) a random sample of 26 stands in which no western gray squirrels were seen (low use); Fort Lewis, Washington, 1992-1993.

Distance ²	Stand use ³		
	High	Moderate	Low
1	44	42	19
2	22	33	8
3	28	17	19
4	5	8	15
5	0	0	38

¹ Statistical results: Minimum expected value = 1.29, Pearson Chisquare = 18.94, df = 8, p = 0.015.

² Distance classes: 1 = < 0.1 km, 2 = 0.1-0.39 km, 3 = 0.4-0.69 km, 4 = 0.7-1.0 km, 5 = > 1.0 km.

³ High use = western gray squirrels were seen in the stand > 2 times or > 2 squirrels were seen in the stand simultaneously; moderate use = squirrels seen in stand 1 or 2 times; low use = squirrels never seen in stand.

most common understory trees were bigleaf maple and Oregon ash. There was no significant difference in total percent cover at the shrub level but species composition varied between high and low use stands. High-use stands had, on average, a greater variety of food-bearing trees and shrubs in the understory (Table 2) and these species, if present, occurred in greater abundance in high-use stands than in low-use stands. Indian plum (*Oemleria cerasiformes*) was significantly more abundant in high-use stands ($p=0.020$) while Scot's broom (*Cytisus scoparius*) was significantly more abundant in low-use stands ($p=0.001$).

High-use stands had significantly more understory oak than low-use stands suggesting more oak regeneration in these stands. At life form level one (forbs, ferns, grasses, and ground-cover), low-use stands had a greater percent of vegetation cover than high-use stands. High-use stands had more ferns ($p=0.010$) and mosses ($p=0.008$) at life form level one, while low-use stands had more grasses ($p=0.020$) and forbs ($p=0.008$). High-use stands had a higher percent cover of coarse woody debris ($p=0.001$) than low-use stands.

Variables we initially thought would be important to western gray squirrels, such as tree density, median DBH of oak, median DBH of Douglas-fir, percent Douglas-fir, percent shrub cover, and amount of hazel, did not vary significantly between high and low-use stands.

Stand Size and Distance to Water: A Test of an Hypothesis

The random sample comparison of the influence of size and distance to water confirmed that squir-

rels indeed preferred larger stands (> 8.0 ha) closer to water (< 0.6 km) than smaller stands further from water (Table 5). The hypotheses of no effects were rejected.

Behavior

We observed squirrels from one minute to five hours at a time. We were able to observe two groups (of 3-7 squirrels each) in two oak stands for 2- and 11- month periods and recorded their activities (Table 6). Primary activities varied seasonally (Figure 3). From November through March, squirrels spent most of their time traveling on the ground and digging for and foraging on buried

TABLE 5. Prospective comparison¹ (number of stands with squirrels/number of stands surveyed) of the number of surveyed *Quercus garryana* stands used by *Sciurus griseus* in 6 size/distance to water categories; 10 stands in each category were chosen randomly from all *Quercus garryana* stands on Fort Lewis, Washington, 1993.²

Size of stand	Distance from water		Total
	<0.6 km	> 0.6 km	
< 2 ha	0/10	0/10	0/20
2-8 ha	0/11	0/10	0/21
> 8 ha	6/11	0/8	6/19
Total	6/32	0/28	6/60

¹ Statistical results: Size x Squirrel $X^2 = 15.73$, $df = 2$, $p = 0.0004$; Water x Squirrel $X^2 = 8.54$, $df = 1$, $p = 0.0035$

² Upon subsequent field examination, two stands were recategorized; one was found to be in a smaller size class and closer to water, and another was closer to water, making sample sizes uneven.

TABLE 6. Time (minutes) western gray squirrels spent at primary activities by month,¹ Fort Lewis, Washington, 1992-1993.

Month	Total time (minutes)	Activity							
		Forage	Travel	Rest	Agonistic	Groom	Watch	Warning/Escape	Mate
January	34	4	27	3	0	0	0	0	0
February	227	67	98	14	19	12	5	12	0
March	168	23	103	2	6	2	0	32	0
April	202	83	46	18	10	4	3	38	0
May	542	2	236	55	208	12	12	13	4
June	38	0	9	0	24	0	4	1	0
August	1362	928	79	81	33	16	18	207	0
September	246	180	30	6	4	2	5	19	0
November	26	4	9	2	0	4	1	6	0
Total	2845	1291	637	181	304	52	48	328	4

¹ Less than 10 minutes of observations were collected in July, October, and December.

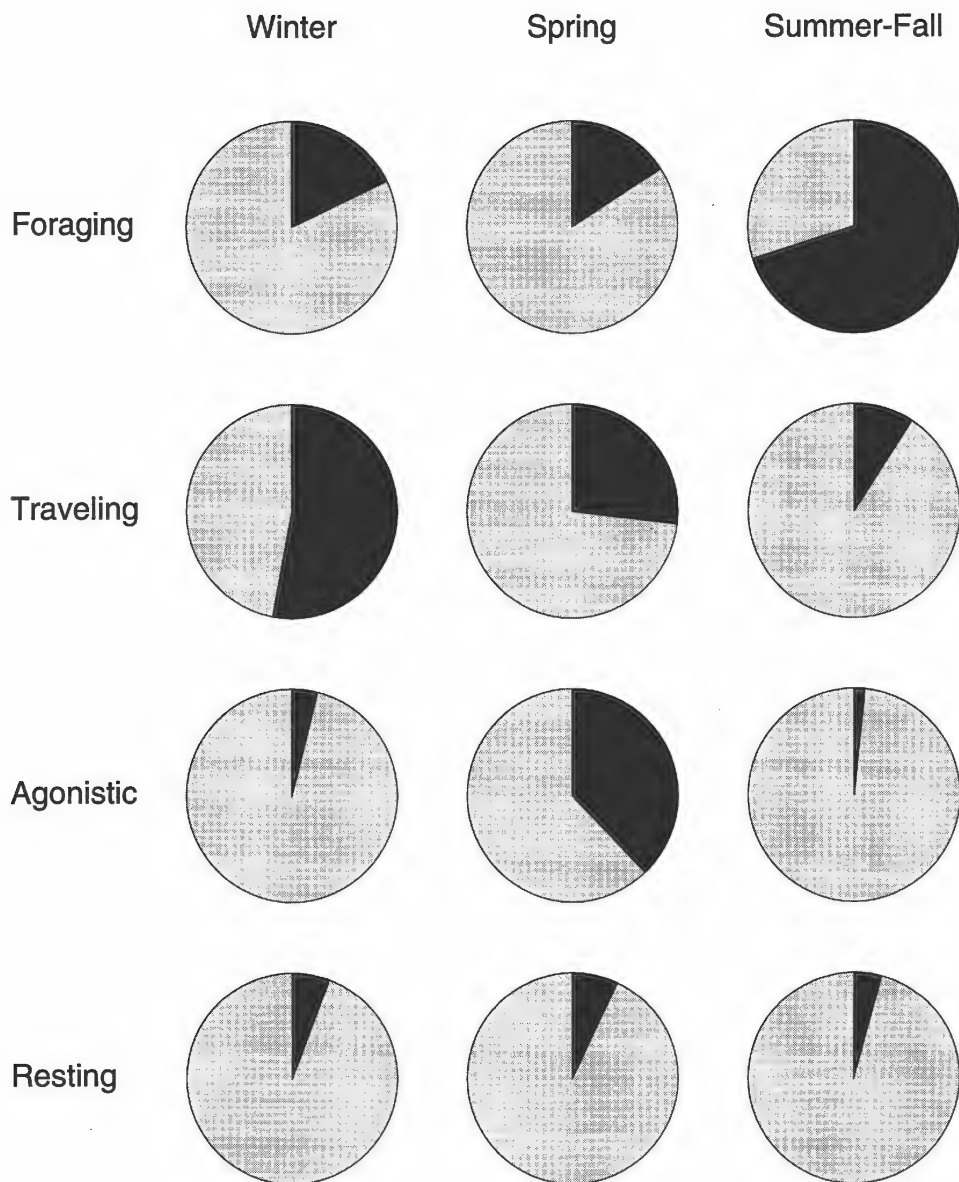


Figure 3. Relative time spent in major out-of-nest activities by *Sciurus griseus*, Fort Lewis, Washington, 1992-1993.

acorns. Travel decreased in late spring and early summer, then increased again in late fall. In April, May, and June, squirrels spent much of their time engaged in agonistic behavior with other western gray squirrels. Sexual behavior was observed in May. From July through October squirrels spent almost all of their out-of-nest time foraging.

The amount of time spent on the ground versus in trees varied significantly among seasons (Table 7). In spring and summer squirrels were seen considerably more often on the ground than in trees (oak and Douglas-fir). In fall and winter squirrels were seen in trees as often as on the ground. Sightings were naturally biased towards roads and the ground since squirrels are more readily seen in the open than in trees. Nevertheless, squirrels frequently traveled on and across roads; 17% (52 of 318) of all squirrel sightings were on paved roads. Twenty-five percent of squirrels seen on roads had been killed by automobiles. This compares with 40% of sightings on the ground, 22% in Douglas-fir, and 16% in Oregon white oak.

TABLE 7. Number of western gray squirrel sightings on the ground and in trees, by season, Fort Lewis, Washington, 1992-1993.

Season ¹	Number of Sightings ²	
	Ground	Tree
Winter	49	51
Spring	70	30
Summer	57	43
Fall	52	48

¹ Winter: December-February, Spring: March-May, Summer: June-August, Fall: September-November.

² Statistical results: Minimum expected value = 19.42, Pearson Chisquare = 8.222, d.f. = 3, p = 0.042

Foraging, including picking, gathering, burying, and eating food items was the most common out-of-nest activity observed overall, especially in August and September when squirrels were gathering and burying acorns in preparation for winter. Squirrels buried each acorn in a separate hole on the ground under or near the source oak tree. In general, food items we saw western gray squirrels eating on Fort Lewis were: 1) spring—fungi, succulent vegetation, and Douglas-fir cambium; 2) summer—bigleaf and vine maple samaras,

and indian plum berries; 3) fall—acorns, Douglas-fir seed, hazelnuts, and fungi; and 4) winter—acorns, hazelnuts, and maple samaras.

Discussion

Distribution and Abundance

Surveys proved effective in locating western gray squirrels and their habitat on Fort Lewis. It is unlikely that we saw all squirrels present in the oak stands we surveyed, but we were able to determine general patterns of distribution. Squirrel distribution followed water courses including streams, rivers, marshes, and lakes—as previously reported by the Washington Department of Wildlife (1993). This type of distribution has been reported for fox squirrels (*Sciurus niger*) in the southeastern United States (P. Weigl, pers. comm. 1994). Distribution of squirrels reflected the size of the oak stand and adjacency of the oak stand to other forests and to water. No squirrels were seen in isolated pure oak stands. Stand size is important in terms of 1) providing an adequate supply of food and nest sites for year-round occupancy, 2) allowing for occupancy of more than one squirrel (the larger the stand, the more squirrels, the greater chance of persistence, and the greater probability the stand will be found by dispersing squirrels); 3) opportunity for diversity in food sources. Adjacency of oak stands to Douglas-fir stands provides additional food and shelter and may provide corridors to other oak patches. Prairie-conifer forest ecotones and water courses are most likely the key dispersal routes for squirrels because squirrels rarely cross open prairies (Barnum 1975).

Western gray squirrels do not appear to be abundant on Fort Lewis. Our best estimate of the number of individual squirrels seen during surveys was 38 (in surveys of 74 % of the oak habitat). This translates to 1 squirrel/13 ha of surveyed oak woodlands. We did not observe squirrels in 82% of the oak forests we surveyed. Combining our survey efforts with squirrel sightings by Fort Lewis personnel, western gray squirrels were found in 44 of 228 oak stands. The low number of occupied stands may reflect three phenomena: the distribution of oak stands over Fort Lewis, including size of stand, distance to water, and adjacency to Douglas-fir; the characteristics of individual stands as they relate to habitat quality (for example,

number of mast-bearing species present); and barriers to dispersal and colonization such as traffic. Oak/Douglas-fir stands are well-distributed across Fort Lewis, but few are known to be inhabited by western gray squirrels (Figure 2).

Habitat Characteristics

The retrospective analysis of 56 oak stands showed that squirrels were seen most often in stands > 2 ha and that were ≤ 390 m away from water. Squirrels were present in most of the large oak stands near water on Fort Lewis but were rarely seen in small (< 2 ha), isolated, and pure oak stands. Our prospective comparison of 60 oak stands showed that western gray squirrels preferred stands > 8 ha and < 600 m from water. Of the 413 oak stands on Fort Lewis, 131 were > 2 ha, and only 63 stands were > 2 ha and ≤ 390 m from water. Only 8 stands were > 8 ha and < 600 m from water. Average summer home ranges of western gray squirrels vary from 2.6 to 4.2 ha (Gilman 1986, Asserson 1974, Foster 1992). Few oak stands on Fort Lewis are > 2.6 ha and within 600 m of water. Squirrels were seen most often in stands with a mixture of conifers, oaks, and other food-bearing tree species. Specific percentages of Douglas-fir and Oregon white oak required to accommodate western gray squirrels are difficult to determine, but squirrels were rarely seen in pure oak stands isolated from Douglas-fir or in pure Douglas-fir stands away from oak. Squirrels were less likely to use stands that are tending towards pure oak; fewer squirrels were seen in stands that had > 50% Oregon white oak than in stands with a greater Douglas-fir component.

The number and variety of food-bearing trees and shrubs in a stand appeared to influence use by western gray squirrels. Bigleaf maple, Oregon ash, and indian plum appeared to be important food-bearing species. The abundance of seed and mast crops varies seasonally, annually, and among species (Nixon et al. 1975); therefore, stands with diverse food sources may provide more stable year-round food supplies for squirrels than stands with few food sources (Gurnell 1983).

High-use stands had more understory trees (which provide vertical routes for travel and escape) than low-use stands. The percent cover of shrubs was not significantly different between low and high-use, but the variety of food-producing shrubs was greater in high-use stands. High-use

stands had more snowberry (*Symphoricarpos albus*), California hazel (*Corylus cornuta*), bigleaf maple, vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), blackberries (*Rubus* spp.), and Oregon ash than low-use stands. Use by squirrels was lower in stands where Scot's broom was most abundant. Scot's broom is a highly invasive species that may quickly take over disturbed areas, prairies, and oak woodlands. Much of the understory of oak woodlands on Fort Lewis, particularly those adjacent to prairies, has been invaded by Scot's broom. Scot's broom can grow over 3 m tall and may create shade conditions unsuitable for the establishment of oak seedlings and other native prairie vegetation. Squirrels are not known to eat the foliage, pods, or seeds of Scot's broom.

The differences in ground vegetation and coarse woody debris between high-use and low-use oak stands appear to be a function of the location of the stand in the conifer forest-oak woodland-prairie mosaic. They may indicate high soil moisture and suitability for fungal production. Low-use oak woodlands had lower basal areas of trees (less tree cover) than high-use stands (Table 2). In general, low-use stands were more open and drier while high-use stands were denser and moister. Grasses were abundant in the dry open oak stands adjacent to prairies, while ferns and mosses were abundant in the moist, denser stands. Coarse woody debris is a characteristic of older interior forests rather than open prairies. Coarse woody debris can provide moist microclimates in otherwise dry areas that allow persistence and fruiting of the sporocarps (truffles) of ectomycorrhizal fungi (Amaranthus 1989).

Behavior

Activities of squirrels appear to vary in response to the breeding season and food availability. The breeding season extends from January to September in western Washington (Brown 1985). The high level of travel in the winter and spring may correspond to the search for mates or for scarce stored food. Agonistic behavior between squirrels in the spring and early summer may be associated with mating in the early spring, and defense of home ranges against dispersing young in the summer.

Food species diversity was an important correlate of squirrel occupancy of oak stands. We

observed western gray squirrels eating a variety of foods as mentioned in the results but there have been few studies of the western gray squirrel diet in Washington. Gaulke and Gaulke (1984) studied western gray squirrels on the Oak Creek Wildlife Recreation Area near Naches, Washington and found that acorns are a major food during February and March and ponderosa pine (*Pinus ponderosa*) seeds a major food in February. They observed squirrels eating large numbers of immature aspen (*Populus tremuloides*) catkins. In California, Stienecker and Browning (1970) determined principle foods by volume: hypogeous fungi, pine nuts, acorns, bay fruit, and green vegetation. Fungi were eaten year-round while pine nuts and acorns were the main summer foods. In southern Oregon, Cross (1969) found that pine seeds, fir seeds, and hypogeous fungi were eaten year-round while acorns were eaten in fall and winter. In northcentral Oregon, squirrels ate fungi, conifer seed, acorns, honeysuckle nectar (*Lonicera coliosa*), and the foliage of miner's lettuce (*Montia perfoliata*) in the spring and summer (Foster 1992). Although previous food habit studies showed that a diversity of food was consumed, they did not demonstrate differences in the variety of foods available in different quality habitats.

The diet of the western gray squirrel is dependent on the seasonal and yearly availability of acorns, conifer seed, fungi, and other foods. The amount of time squirrels spend on the ground versus trees also depends on the kinds of food that are available. For example, Foster (1992) observed most foraging on the ground, except in the fall when squirrels were gathering acorns from oak trees. We observed similar patterns in foraging. Most of the year, squirrels must leave the safety of trees to forage on the ground for food. Western gray squirrels do not discriminate against roads during on-the-ground travel and 25% of squirrels seen on roads were dead. Roads (particularly those with heavy traffic) are a threat to the continuing persistence of western gray squirrels. Many deaths on roads occurred in the spring when females were pregnant and, again, in summer when young were dispersing.

Management Implications

Management for the western gray squirrel should involve protecting both the squirrel and its habitat. The greatest threats to western gray squirrels

on Fort Lewis appear to be habitat loss due to succession and invasion by Douglas-fir, the over-dispersion of oak woodlands, and automobile traffic. Raising public awareness of the presence and status of the western gray squirrel through brochures and posted road signs may reduce squirrel deaths on roads. Active management is critical in preserving dwindling oak woodlands.

Oak communities in other parts of Washington were diminished in the past by the removal of oak for firewood, agriculture, and grazing. They have been further reduced because of fire suppression (leading to succession by Douglas-fir), logging, and the clearing of trees for housing developments. Oak-conifer forest has high value for western gray squirrels because it provides a variety of food, cover, and nest sites (Gilman 1986). Oak provides travel ways (Foster 1992), food (in the form of acorns and edible truffles; Molina 1992), and escape cover. Conifers (Douglas-fir on Fort Lewis) provide year-round cover, nest sites (Cross 1969, Foster 1992), cone seed, and truffles (Luoma 1991). No other communities seem to support western gray squirrels in western Washington.

Oak-conifer forests are transitional communities that require continued management for their maintenance. Oregon white oak stands may be replaced by faster growing Douglas-fir and, then, by climax stands of grand fir (*Abies grandis*) or grand fir and Douglas-fir (Franklin and Dyrness 1988). On Fort Lewis, this succession to Douglas-fir is evident in most oak stands except for those that are isolated from conifers and that have little value for western gray squirrels. There is little evidence of succession from Douglas-fir to grand fir on Fort Lewis.

Our study showed that squirrels preferred large stands near water. Therefore, management should emphasize preserving oak stands that are > 8 ha and that are < 600m from water. Small stands near water and adjacent to coniferous forests are high-priority candidates for management to increase the area of oaks. Mature, acorn-producing oaks can be maintained by killing over-topping trees by girdling or felling. Growth of smaller oaks can be encouraged by releasing them from competition with conifers. Reducing competition with oak seedlings, Scot's broom, young Douglas-fir, and invading grasses thus may be important both in allowing oaks to regenerate and in preserving native

prairies. Management may include prescribed burning on prairie edges to control the invasion of Scot's broom and retain native plant species. Franklin and Dyrness (1988) report that fires set by native Americans (before European settlement) reduced the invasion by Douglas-fir and lessened the amount of brush in oak woodlands thus creating a park-like appearance.

Western gray squirrels on Fort Lewis used stands with native understory vegetation over those with Scot's broom understory. Because squirrels did not use isolated oak stands, were often killed by crossing roads, and would be highly vulnerable to predation when away from trees, we believe that once oak stands are being maintained, the next priority is to protect habitat corridors between oak patches to facilitate travel by squirrels. Adding water sources such as small man-made ponds or guzzlers (Schemitz 1980) to oak stands that are large and adjacent to conifer stands could significantly increase the amount of suitable squirrel habitat.

Maintaining a mix and juxtaposition of habitat conditions is necessary to maintain western gray squirrel populations. Fort Lewis is an important area for western gray squirrel management because it holds the largest publicly managed area of Oregon white oak in the Puget Sound

region. The problem of diminishing oak communities is not unique to Fort Lewis. Oregon white oak woodlands have diminished throughout western Washington, Oregon, and California. Conservation of oak communities, and, thus the western gray squirrel, must involve the cooperation of county, state, and federal agencies and public land owners (Bleier et al. 1993). Fort Lewis foresters currently manage for the maintenance of prairies, wetlands, oak woodlands, and continuous cover variable-age conifer forests. All these habitat conditions are beneficial to western gray squirrels.

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Literature Cited

- Amaranthus, M. P., D. S. Parrish, and D. A. Perry. 1989. Decaying logs as moisture reservoirs after drought and wildfire. In E. Alexander (ed.) Stewardship of soil, air, and water resources, proceedings of watershed 89. USDA For. Serv. Alaska Region. Publ. R10-MB-77.
- Asserson, W.C., III. 1974. Western gray squirrel studies in Kern County, California. California Department of Fish and Game, Sacramento. Admin. Rep. 74.1. 32 p.
- Barnum, D. A. 1975. Aspects of western gray squirrel ecology. M. S. Thesis, Wash. State Univ., Pullman. 55 p.
- Bleier, C., C. Bolsinger, L. Huntsinger, D. D. McCreary, P. Muick, R. Schmidt, T. A. Scott, R.B. Standiford, T. Swiecki, and W. Tietje. 1993. A planner's guide for oak woodlands. Integrated Hardwood Range Management Program, Univ. of Calif., Berkeley. 94 p.
- Bowles, J. H. 1921. Notes on the California gray squirrel (*Sciurus griseus griseus*) in Pierce County, Washington. Murrelet 2:12-13.
- Brown, E. R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 2: Appendices. USDA, For. Serv. R6-F&WL-192-198. Pacific Northw. Region, Portland, Ore. 302 p.
- Carraway, L. N. and B. J. Verts. 1994. *Sciurus griseus*. Mammalian species 474:1-7
- Cottam, G. C., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecol. 37(3):451-460.
- Cross, S. P. 1969. Behavioral aspects of western gray squirrel ecology. Ph.D. Diss., Univ. of Arizona, Tucson. 168 p.
- Foster, S. A. 1992. Studies of ecological factors that affect the population and distribution of the western gray squirrel in northcentral Oregon. Ph.D. Diss., Portland State Univ. 154 p.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-8, Pac. Northw. For. Range Exp. Sta. 417 p.
- Gaulke, J. A., and P. A. Gaulke. 1984. Status of the western gray squirrel population in the Oak Creek Wildlife Area. Wash. Dep. Wildl., Yakima. 15 p.
- Gilman, K. N. 1986. The western gray squirrel (*Sciurus griseus*), its summer home range, activity times, and habitat usage in Northern California. M. S. Thesis, Calif. State Univ., Sacramento. 71 p.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal. Rev. 13 (2/3/4):133-148.
- Hitchcock, L. C., and A. Cronquist. 1991. Flora of the Pacific Northwest. Univ. of Wash. Press, Seattle. 730p.

- Molina, R., H. Massicotte, and J. M. Trappe. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: *Mycorrhizal Functioning: An Integrative Plant-Fungal Process*. New York: Chapman and Hall. 423 p.
- Nixon, C. M., M. W. McClain, and R. W. Donahoe. 1975. Effects of hunting and mast crops on a squirrel population. *J. Wildl. Manage.* 39:125.
- Rodrick, E. A. 1987. Survey of historic habitats of the western gray squirrel (*Sciurus griseus*) in the south Puget Trough and Klickitat County, Washington. M. S. Thesis, Univ. of Wash., Seattle. 41 p.
- Schemitz, S. D. 1980. *Wildlife Management Techniques Manual*. The Wildlife Society, Inc., Wash., D.C. 686 p.
- Stein, W. I. 1990. (*Quercus garryana*) Dougl. ex Hook Oregon white oak. Pages 650-660 in Burns, Russell M. and B. H. Honkala, tech. coords. *Silvics of North America*, Vol. 2: Hardwoods. Agricultural Handbook 654.
- Stienecker, W. E., and B. M. Browning. 1970. Food habits of the western gray squirrel. *Calif. Dep. Fish. Game*: 56:36-38.
- Washington Department of Wildlife. 1993. Status of the western gray squirrel (*Sciurus griseus*) in Washington. Final status report. Wash. Dep. of Wildl., Olympia. 36 p.

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and

Robert H. Naney, U.S. Forest Service, Okanogan, Washington 98840

Response of Coyotes and Gray Wolves to Simulated Howling in North-central Washington

Abstract

Simulated howling provided information on the location of coyotes (*Canis latrans*) and gray wolves (*Canis lupus*) in north-central Washington. Coyotes responded to simulated howling at a rate of 9.9% and wolves at a rate of 0.1% from April through October. The low response rate for wolves can most likely be attributed to low density in our study area. Response rates of coyotes were highest in September and October, and during dawn and dusk. Both wolf responses occurred during early August and at dusk. The sex of the person simulating the howl did not affect the response rate. There was not a significant difference in the response rates of coyotes between backcountry and road surveys. Monitoring the RR/S of these species may be useful in estimating the response of coyotes to a recolonizing wolf population. This method would be a useful component in programs monitoring the populations of wolves and coyotes.

Introduction

Simulated howling surveys have been used to locate wolves and coyotes, to estimate changes in the numbers of packs and pack size (Joslin 1967, Pimlott and Joslin 1968, Theberge and Strickland 1978), and to provide indices of canid abundance (Carbyn 1982, Fuller and Sampson 1986). Harrington and Mech (1982) presented a methodology for a saturation census and a sampling census using simulated howling surveys. Fuller and Sampson (1986) applied the sampling census over a relatively small area where information on wolf numbers and/or locations were available from radio telemetry studies. Tucker et al. (1990) discussed the application of howling surveys as one of several survey methods that can be used to locate canids. Very few studies have applied this methodology to determine coyote locations and response rates (Carbyn 1982, Laundre 1981, Pesendorfer et al. 1986), and it has never been applied to such a large study area.

The purpose of our study was to use simulated howling to indicate the presence and general location of gray wolves and coyotes within our study area, generally following the sampling census method (Harrington and Mech 1982). The limitations of howling surveys have been discussed in several publications (Fuller and Sampson 1986, Harrington and Mech 1982, Tucker et al. 1990) and we considered these in the design of our project.

The howling surveys discussed in this paper were used in conjunction with the other methods discussed by Tucker et al. (1990).

The specific objectives of this study were to locate wolves and coyotes, evaluate the effects of the time of day, time of the year, the sex of the person conducting the simulated howls, and backcountry vs road surveys on their response rates. We also provide recommendations on the application of this method to a large study area.

Study Area

The study area included all of the Okanogan National Forest west of the Okanogan and Columbia rivers and that portion of the Wenatchee National Forest north of Interstate 90 (Figure 1), all within north-central Washington state. The study area is bounded on the north by the US/Canadian border, on the west by the crest of the North Cascades mountains, on the south by the Interstate 90 highway corridor, and on the east by the Columbia and Okanogan rivers. The study area is about 890,340 hectares in size.

The study area is comprised of 22% designated wilderness areas that are accessed solely by trails. The remaining portion of the study area is multiple use national forest lands. An extensive network of roads provide access into this portion of the study area.

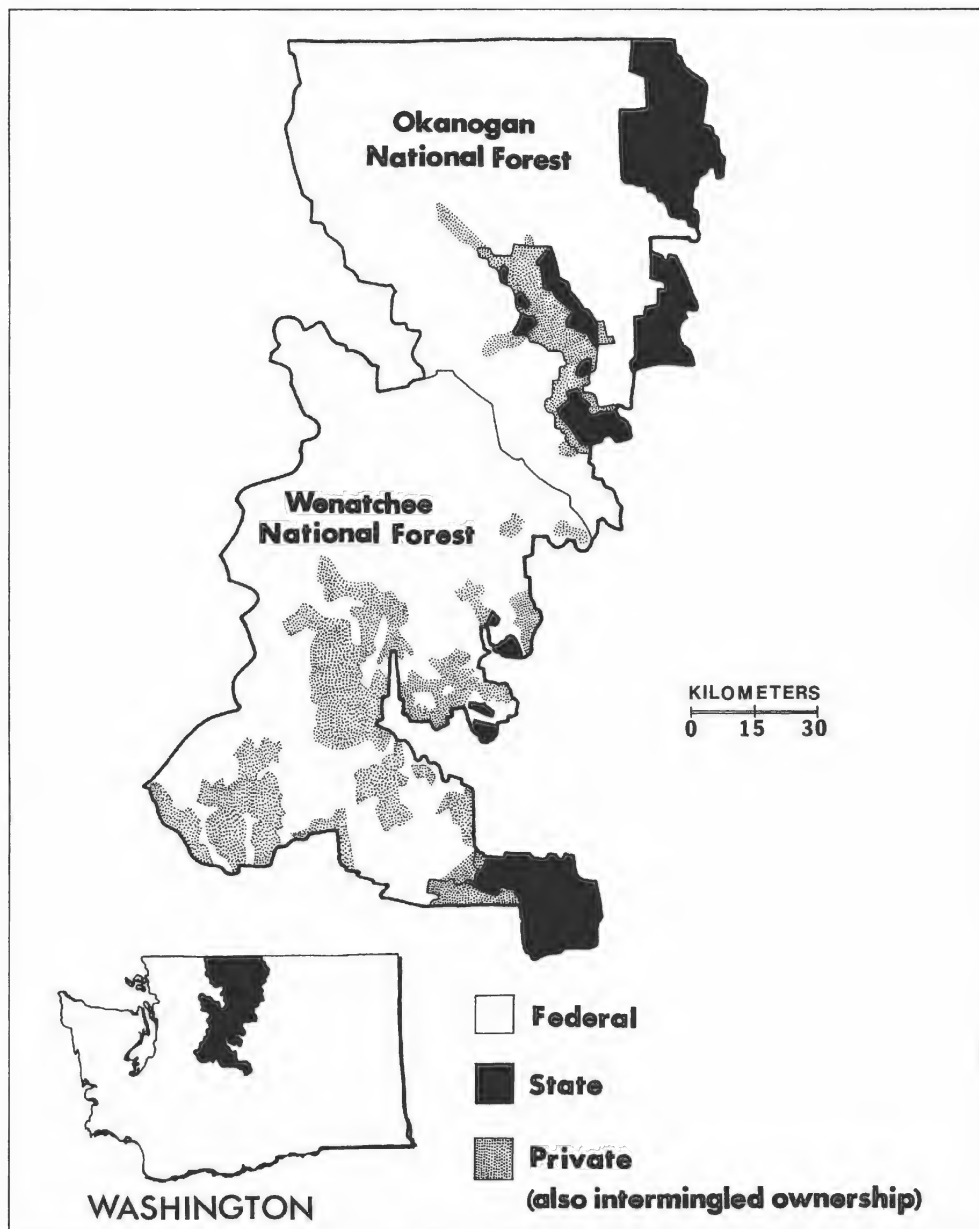


Figure 1. Map of the study area.

The elevations range from about 2300 meters along the Cascade crest to 500 meters along the eastern boundary of the study area. Precipitation levels vary from 300 cm/year in some areas along the Cascade crest to 25 cm/year in the dry east side of the study area.

Methods

We used the methodology presented by Harrington and Mech (1982) to locate gray wolves and coyotes within our study area. In general, this method involved locating howling stations approximately 1.6 km apart. We spatially stratified our study area by historical wolf presence (within past five years as determined by the Washington Department of Fish and Wildlife Large Carnivore Investigations team), ungulate winter/spring range, or recent reliable sightings that were evaluated by an interagency team.

Stations and routes were designed to limit water noise from creeks and rivers and account for varied topography. Each station was designed to cover approximately 2.6 km², following Fuller and Sampson (1986). At each station one person conducted a howling trial that consisted of three to five howls alternating "flat" and "breaking" howls over a period of 20 to 35 seconds. This was repeated two times with a two minute interval in between each howling trial to complete one howling session. Harrington and Mech (1982) recommended three trials, the first being of lower volume, but showed higher response rates for the last two trials. We used two trials to reduce the time at each station and covered more of our study area. We always used live human imitations of howls, as research has shown this to work as well or better than playbacks of recorded wolf howling (Theberge and Falls 1967).

Howling sessions were not conducted when there was precipitation or wind >10 km/hour. The information recorded during each howling trial included time, sex of howler, response on first or second vocalization, suspected species of canid, and weather conditions. Surveys were conducted April through October from 1991 to 1993. Survey efforts were most intensive during the months of July, August, and September, as recommended by Harrington and Mech (1982).

When survey routes occurred along roads we followed the recommendations of Harrington and Mech (1982) and Tucker et al. (1990) by con-

ducting surveys on three consecutive nights. However, when survey routes occurred in the backcountry we did not follow the three consecutive night routine. Instead we adopted a method developed in consultation with P. Paquet and R. Ream that maximized the area covered by only surveying for one night. Backcountry routes followed trails or ridges and stations were spatially located at distances similar to road surveys.

Field crews carried tape recorders equipped with parabolic microphones (Bionic Booster, Silver Creek Industries, Manitowol, WI. 54220) to record any responses. All responses were recorded on tape for later verification of canid species by an interagency team of biologists. Species were differentiated by the aural characteristics of their howls. Fundamentally, wolf howls differ from coyote howls in pitch, intensity, and duration (Theberge and Falls 1967).

We evaluated the responses of canids using the parameter of Response Rate per Session (RR/S) and Response Rate per Trial (RR/T) (Harrington and Mech 1978a). The RR/S was the percent of howling sessions during which replies were received and the RR/T was the percent of the howling trials that were answered during a howling session (Harrington and Mech 1978a). The RR/S was calculated at two hour time intervals from 1800 to 0800 in order to estimate diurnal fluctuations. By using these parameters the response rate was standardized allowing monthly comparisons of RR/S even though survey efforts varied depending upon weather conditions and available personnel.

Results and Discussion

Presence and General Location

The presence of coyotes determined from the howling surveys was confirmed at 213 locations and occurred throughout the study area. Coyotes were located in a variety of habitats, including areas that received relatively high levels of human use. Wolves were located in two areas using simulated howling. Both of these locations occurred in designated wilderness areas where human activities were relatively low. A more detailed discussion of habitat use and the effects of human activities is beyond the scope of this project.

Overall Response Rate

A total of 2137 howling sessions were conducted resulting in 215 responses by canids and an overall RR/S of 10%. Of the total number of canid responses, two were determined to be wolf and 213 were coyotes. The RR/S of wolves was very low (0.1%) and is likely due to low numbers of wolves in the study area. The RR/S of coyotes was 9.9%.

Of the coyote responses, 27% were made by lone animals, 73% by packs of two or more animals. Further differentiation of group numbers is extremely difficult (Harrington and Mech 1982). One of the wolf responses was made by a lone animal and the other by a pack of more than two animals.

Canid responses were analyzed to determine the proportion that occurred on the first or second trial. The response on the first howling trial was 65%, and 35% on the second trial. Both wolf responses occurred during the first howling trial, one response was from a wolf pack and one by a lone animal. Harrington and Mech (1982) reported a response rate of 68% by wolves on the first trial. Our results indicated that the response rate of coyotes is similar.

Time of Day

The RR/S for two hour time intervals from 1800 to 0800 PST are shown in Figure 2. During two time periods, 1800 and 2000 PST and between 0400 and 0600 PST, the RR/S for coyotes was 16% and 11%, respectively, above the overall RR/S. The lowest RR/S occurred between 0201 and 0400 PST (6%) and between 0601 and 0800 PST (0%). The wolf responses occurred during the 2201 to 2400 PST period. These results are similar to those reported in other studies where peaks in howling frequency by gray wolves occurred during the evening and morning hours (Harrington and Mech 1978b).

Time of Year

We limited our survey season to April through October. This corresponds to one of the high response rate periods reported by Harrington and Mech (1982). The RR/S of coyotes increased spring through fall (Figure 3). RR/S of coyotes was highest during the months of September (11%) and October (12%), and lowest in the spring. Harrington and Mech (1978b) reported a seasonal increase in howling frequency for two wolf packs they monitored. Harrington and Mech (1982) showed

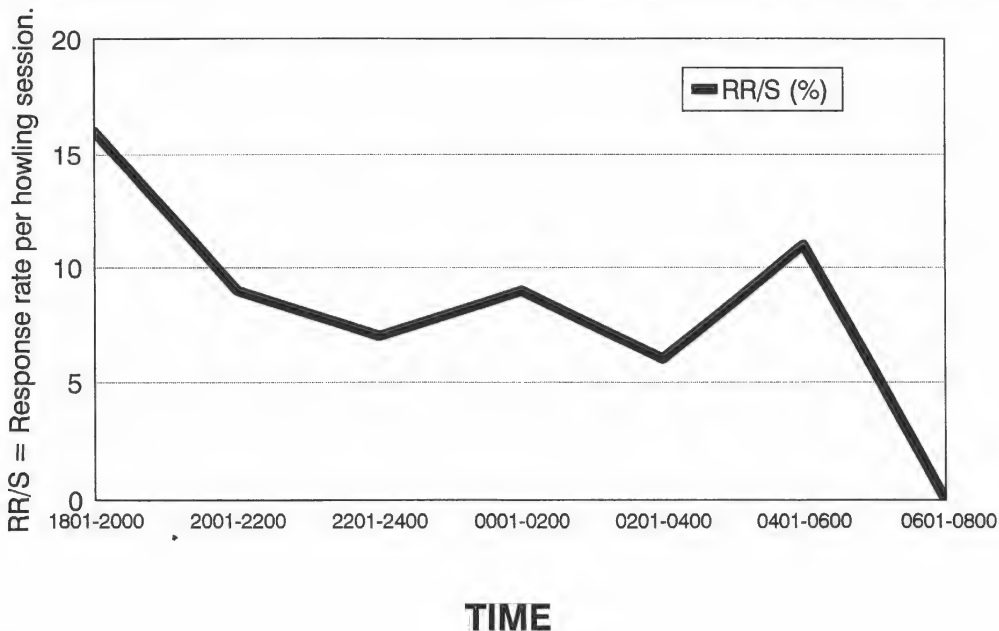


Figure 2. Diurnal response rates of coyotes.

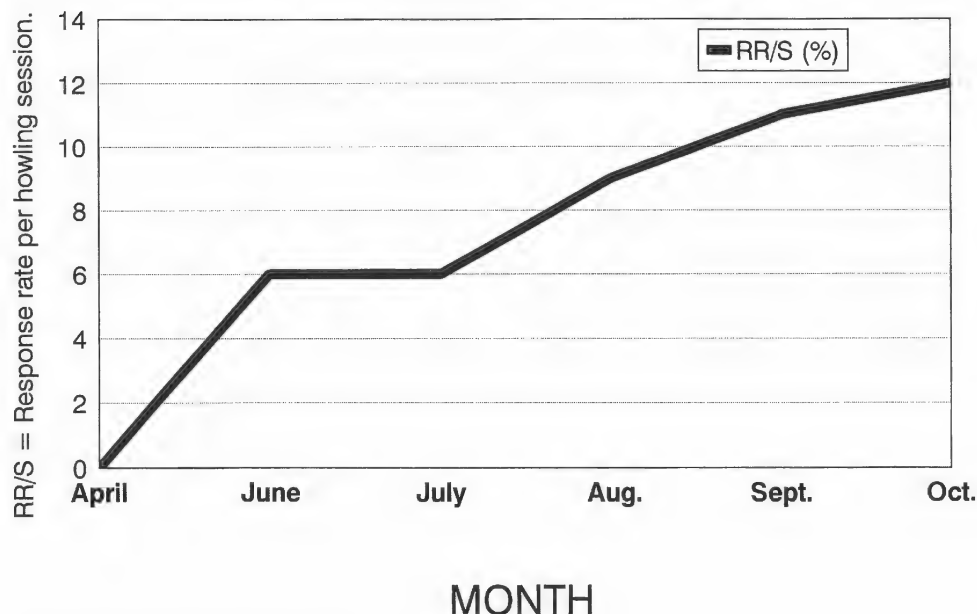


Figure 3. Monthly response rates of coyotes.

that wolf packs were more responsive to simulated howling during the summer and fall. Joslin (1967) reported a seasonal increase in responses by wolves to simulated howling and attributed the higher response rates to increased pup responsiveness. Our results and observations indicated that the seasonal increase in RR/S by coyotes may also be related to increased activity by pups. The two responses from gray wolves occurred during early August.

Sex of Howler

There was not a significant difference between the RR/S by coyotes relative to the sex of the howler. When females conducted the howling session, the RR/S was 9.8% ($p < 0.05$), and RR/S was 11.0% ($p < 0.05$) when conducted by males. One wolf response was elicited by a male howler and one by a female.

Backcountry vs Road Surveys

Most of the surveys were conducted from roads (85%) vs trails (15%) due to the ease of access. However, there was not a significant difference in the RR/S by coyotes between howling surveys conducted from roads (RR/S = 8.4%, $p < 0.05$)

or from trails (RR/S = 10.3%, $p < 0.05$). Both of the responses by wolves occurred while conducting backcountry surveys.

Conclusions

Fuller and Sampson (1986) and Crete and Messier (1987) felt that howling surveys conducted over large areas were infeasible due to logistical and statistical restraints. We feel that, given funding and available personnel, application of this method over large areas can produce results that may be of use to resource managers and researchers. Our suggestions for conducting a survey of coyotes and wolves closely follow those of Harrington and Mech (1982). They made the following recommendations: (1) the best times of the day are dawn and dusk; (2) July, August, and September are the best months; and (3) trials should be repeated three times at two minute intervals (Harrington and Mech 1982).

Based upon the results of our study, howling surveys for coyotes and wolves can be effectively conducted from June through October. The highest response rates occurred in September and October. However, locations made during June and July provided information about den and

rendezvous sites. Surveys are best conducted during the dawn and dusk hours. Because a high proportion of the canid responses did not occur until the second howling trial, we suggest at least two trials/session. We also discovered that the sex of the person simulating the howls did not affect the RR/S of coyotes.

The RR/S of coyotes was not significantly different between road and backcountry howling survey strategies. This may be a function of the coyotes' tolerance of human activities but also suggests that our one-time survey strategy was an adequate method to elicit coyote responses. Our information was inconclusive relative to RR/S by wolves from roads vs backcountry routes. However, other studies have documented the negative effects that roads can have on wolves (Fuller 1990, Mech et al. 1988). Both of the responses by wolves in this study occurred while conducting backcountry surveys.

The use of simulated howling to elicit responses of coyotes and wolves in our large study area was

successful in verifying the presence of many coyotes and gray wolves at two locations. The application of the methodology to such a large study area was very labor intensive. However, we feel that the RR/S reported here accurately reflects the relative abundance of the two species and can be used as an index to monitor trends. Monitoring the RR/S of these species may be useful in estimating the response of coyotes to a recolonizing wolf population, and as one technique that can be used to monitor the populations of gray wolves and coyotes.

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Literature Cited

- Carbyn, L. N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. *Can. Field Nat.* 96:176-183.
- Crete, M., and F. Messier. 1987. Evaluation of indices of gray wolf density in hardwood-conifer forests of southwestern Quebec. *Can. Field Nat.* 101:147-152.
- Fuller, T. K. 1990. Dynamics of a declining white-tailed deer population in north-central Minnesota. *Wildl. Monogr.* No. 110.
- Fuller, T. K., and B. A. Sampson. 1986. Evaluation of a simulated howling survey for wolves. *J. Wildl. Manage.* 52(1):60-63.
- Harrington, F. H., and L. D. Mech. 1982. An analysis of howling response parameters useful for wolf pack censusing. *J. Wildl. Manage.* 46(3):686-693.
- _____. 1978a. Wolf howling and its role in territory maintenance. *Behaviour* LXVIII,3-4:207-248.
- _____. 1978b. Howling at two Minnesota wolf pack summer homesites. *Can. J. Zool.* 56(9):2024-2028.
- Joslin, P. W. B. 1967. Movements and homesites of timber wolves in Algonquin Park. *Am. Zool.* 7:279-288.
- Laundre, J. W. 1981. Temporal variation in coyote vocalization rates. *J. Wildl. Manage.* 45:767-769.
- Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildl. Soc. Bull.* 16:85-87.
- Pesendorfer, J., P. C. Paquet, and L. N. Carbyn. 1986. Comparison of 1984 and 1985 nocturnal howling surveys in Riding Mountain National Park, Manitoba. *Can. Wildl. Ser. No. 18.* 18pp.
- Pimlott, D. H. and P. Joslin. 1968. The status and distribution of the red wolf. *Trans. N. Amer. Wildl. and Nat. Res. Conf.* 33:373-389.
- Theberge, J. B., and D. R. Strickland. 1978. Changes in wolf numbers, Algonquin Provincial Park, Ontario. *Can. Field Nat.* 92:395-398.
- Theberge, J. B., and J. B. Falls. 1967. Howling as a means of communication in timber wolves. *Am. Zool.* 7:331-338.
- Tucker, P. A., D. L. Davis, and R. R. Ream. 1990. Wolves: Identification, Documentation, Population Monitoring and Conservation Considerations. No. Rockies Nat. Res. Center.

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Offshore Distances of Gray Whales Migrating Along the Oregon and Washington Coasts, 1990

Abstract

Aerial surveys were conducted during January and March, 1990, to determine the width of the gray whale (*Eschrichtius robustus*) southbound and northbound migration corridors along Oregon and Washington. Migrating gray whales occurred significantly farther offshore during the southbound migration compared to the northbound migration. Also, whales occurred significantly farther offshore Washington than Oregon during both migration periods, which we attribute to a portion the whales following a more direct offshore route between approximately the Columbia River mouth and central Vancouver Island rather than a longer nearshore route past Cape Flattery. When compared with previous studies, the migration corridor along the coasts of Oregon and Washington appears to be both seasonally and annually elastic, and in some locations expanding as far offshore as 43 km. These results question the feasibility of conducting accurate shore-based gray whale censuses along these coasts because of the high proportion of whales traveling beyond a shore-based observer's range of view. These results also suggest that the migration corridor is sufficiently wide, especially during the southbound migration, that it might overlap potential offshore oil development areas on the continental shelf.

Introduction

Nearly the entire population of approximately 21,000 (Breiwick et al. 1988) gray whales (*Eschrichtius robustus*) passes through the waters off Oregon and Washington twice yearly while migrating between winter calving lagoons in Mexico and summer feeding grounds in the Bering and Chukchi seas (Wolman 1985). The southbound migration generally peaks off Oregon and Washington during December and January with approximately 90% passing Yaquina Head, Oregon, between December 19 and January 23 (Herzing and Mate 1984). The first phase of the northbound migration peaks in mid-March, typically followed 7 to 9 weeks later by a second (cow/calf) phase (Herzing and Mate 1984).

Migrating gray whales generally travel close to shore, remaining within 3 km throughout most of the route (Hessing 1981, Braham 1984, Rugh 1984, Herzing and Mate 1984, Brueggeman et al. 1987, Breiwick et al. 1988). For instance, land-based observations by Herzing and Mate (1984) indicated that nearly all southbound and northbound (first phase) migrants passed within 5 km of Yaquina Head, Oregon, from 1978-1981. However, gray whales have been observed traveling

through the Channel Islands 80-200 km from the southern California mainland (Rice 1965, Rice and Wolman 1971, Leatherwood 1974, Kent et al. 1980, Jones and Swartz 1987) following a more direct route past the California Bight. Also, Poole (1984) observed that the first phase of northbound migrators in California traveled a straight-line route past Estero Bay while the second cow/calf phase followed the longer coastal corridor inside the bay. Furthermore, in the 1960s, Wilke and Fiscus (1961) and Pike (1962) observed numerous gray whales migrating 8 to 28 km offshore of the Columbia River mouth and the Washington outer coast, and Pike (1962) reported a single sighting of 3 whales 37 km west of Cape Flattery.

In 1989-1990, we conducted aerial surveys for marine fauna (marine mammals, seabirds, and sea turtles) occurring within 185 km of the Oregon and Washington coasts as part of an impact assessment of potential offshore oil development. One objective of the study was to determine the breadth of the gray whale migration corridor along Oregon and Washington relative to the 1990 southbound and first wave of the northbound migration periods to identify where the corridor might overlap with potential oil development areas. This paper reports the results of this investigation.

Study Area and Methods

Aerial surveys were conducted during 3-12 January (southbound gray whale migration) and 11-16

¹Current address: Parametrix Inc., 5808 Lake Washington Blvd. NE, Kirkland, WA 98033

²Current address: Olympic Coast National Marine Sanctuary, 138 W First St., Port Angeles, WA 98362

March (first phase northbound), 1990, along 32 east-west oriented transect lines located between Cape Flattery, Washington, and the Oregon/California border. Spacing between transect lines varied to ensure coverage of areas where marine mammals and seabirds are known to concentrate (bays, river mouths, oceanic banks, etc.), but averaged approximately 22 km. Transect line lengths also varied with 75% of them extending from the coast to the 1,000-m isobath (50-75 km offshore) and 25% extending from the coast to 185 km offshore. This variation in line lengths were established to limit survey effort in typically less productive offshore waters.

Surveys were flown in a 300-series DeHavilland Twin Otter aircraft equipped with bubble windows providing forward and downward visibility. The marine mammal survey team consisted of two observers (one located on each side of the aircraft) and a data recorder. Surveys were flown at a 60-m altitude and a 185 km/hr ground speed.

Statistical comparisons between migration periods and between states (Oregon and Washington) were made using Student's *t*-test (Zar 1974). Centers and directions of migration corridors were approximated using linear regression (Neter and Wasserman 1974). Data were log-normal transformed before analysis.

Results

A total of 44 groups of 85 gray whales were observed during the January 1990 survey of the southbound migration and 68 groups of 124 whales during the March 1990 survey of the first wave of the northbound migration. Nearly 66% of the southbound migrating groups were >10 km from shore compared to 24% of the northbound groups (Figure 1). Gray whales occurred significantly ($t = 4.78$, $p < 0.0001$) farther from shore during the southward migration ($\bar{x} = 14.3 \text{ km} \pm 8.2 \text{ SD}$) relative to the northward ($\bar{x} = 8.0 \text{ km} \pm 3.9 \text{ SD}$).

Gray whales occurred significantly ($t = 3.10$, $p < 0.007$) farther offshore Washington ($\bar{x} = 18.5 \text{ km} \pm 11.9 \text{ SD}$) than Oregon ($\bar{x} = 9.2 \text{ km} \pm 4.2 \text{ SD}$) when data from both migration periods were combined. This difference was especially apparent during the southbound migration when Washington observations ($\bar{x} = 25.2 \text{ km} \pm 13.2 \text{ SD}$) were on average over 13 km farther offshore than Oregon observations ($\bar{x} = 11.9 \text{ km} \pm 3.9 \text{ SD}$; $t = 2.81$, $p < 0.025$). Differences during the north-

bound migration period were less significant ($t = 2.21$, $p < 0.059$) although Washington sightings ($\bar{x} = 11.8 \text{ km} \pm 5.4 \text{ SD}$) still averaged over 4 km farther offshore than Oregon sightings ($\bar{x} = 7.5 \text{ km} \pm 3.4 \text{ SD}$). The farthest offshore distance during the southbound migration off Washington was 43 km (5 groups) and off Oregon 23 km (2 groups). During the northbound migration the farthest offshore sightings were 20 km off Washington (1 group) and 19 km off Oregon (1 group).

The linear regression analysis showed that the center of both the southbound ($r^2 = 0.0003$) and northbound ($r^2 = 0.033$) corridors did not change in respect to latitude off Oregon, while off Washington the distance whales traveled from shore increased dramatically with increasing latitude during both migration periods (southbound, $r^2 = 0.803$; northbound, $r^2 = 0.636$) (Figure 2).

All whales observed on full-effort (2 observers at full attention) transects migrating past Washington were >5 km offshore. Eight whales, however, were incidentally observed migrating within 5 km of the Washington coast during transit flights. Although gray whales were generally found closer to shore along the Oregon coast, only 16% of these whales were observed within 5 km.

Discussion

Although gray whale migration patterns are relatively predictable with respect to timing and location, the extent of the migration corridor may change annually. Our observations off Oregon (only 16% of all whales passing within 5 km of shore) are in contrast with Herzing and Mate's (1984) shore-based observations of nearly all southbound and first phase northbound migrants passing within 5 km of Yaquina Head, Oregon, suggesting a change in the offshore distribution has occurred since their study ended in 1981. Past studies have also suggested that the width or location of the migration corridors may fluctuate over time. For instance, Hubbs (1959) and Rice and Wolman (1971) suggested that the few whales observed along traditional migration routes off California in the late 1800s and early 1900s (Townsend 1887, Andrews 1914, Howell and Huey 1930) was due to animals traveling farther offshore to avoid shore-based whaling pressure rather than an overall population decline.

That gray whales migrate within 5 km past Cape Flattery can not be refuted based on

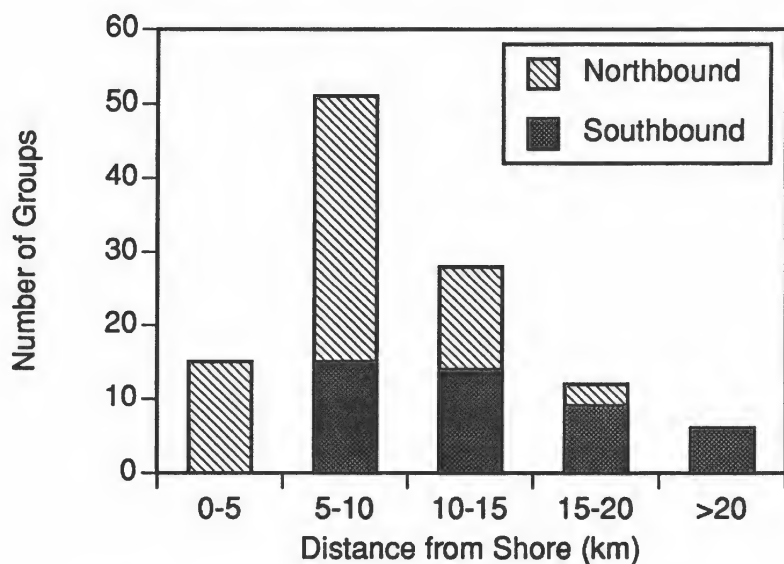
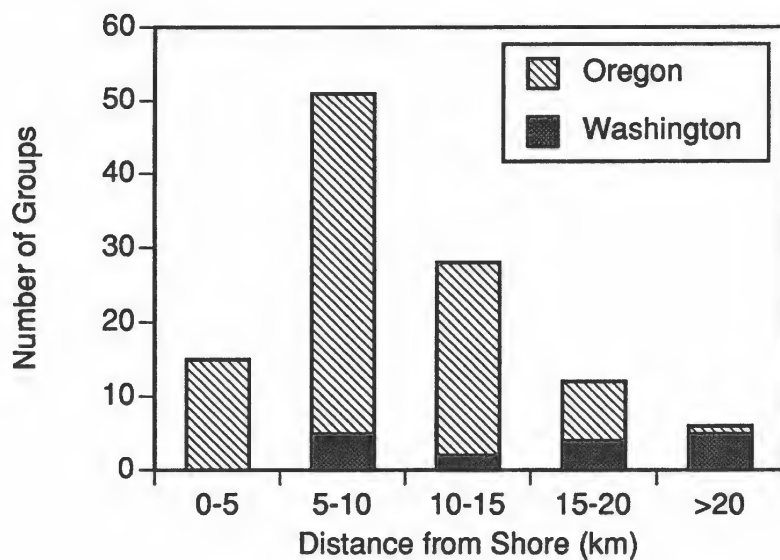


Figure 1. Distances from shore of migrating gray whales comparing between Oregon and Washington, and between the southbound and first phase of the northbound migrations, 1990.

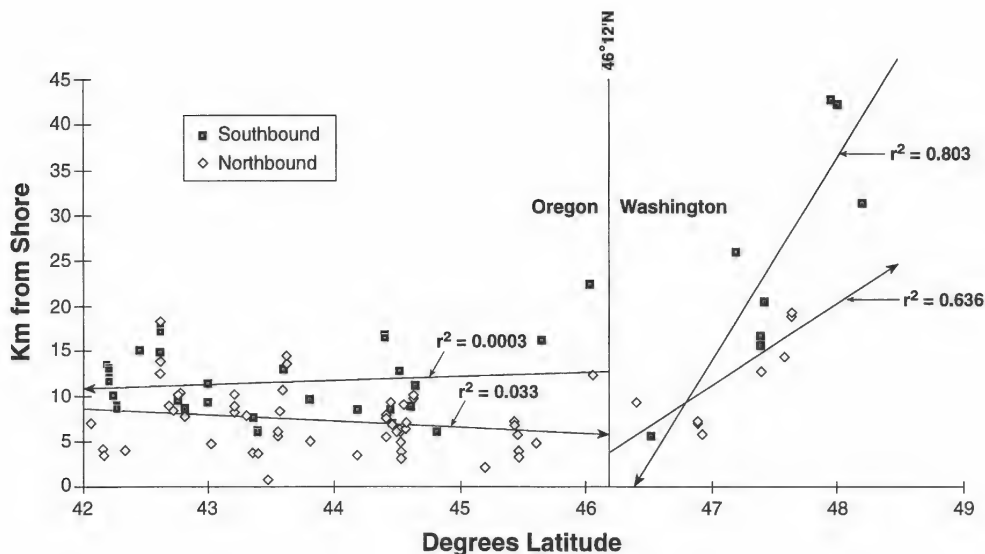


Figure 2. Distribution and mean directions of travel for gray whales migrating along the coasts of Oregon and Washington, 1990.

observations by Pike (1962) and Hatler and Darling (1974). However, our sightings of whales traveling 5-43 km offshore of Washington coupled with observations by Wilke and Fiscus (1961) and Pike (1962) of whales traveling 9-37 km off Washington support the occurrence of either a single, very broad corridor or an alternate offshore route. We suggest that some portion of the population take a more direct route to and from the central coast of Vancouver Island thereby avoiding the longer coastal route past Cape Flattery. Previous researchers in California have noted migrating whales following more direct routes past coastal indentations such as the California Bight (Rice 1965, Rice and Wolman 1971, Leatherwood 1974, Kent et al. 1980, Jones and Swartz 1987) and Estero Bay (Poole 1984). The Washington offshore route also allows whales to cross the deep (250-650 m) Juan de Fuca submarine canyon at its narrowest point (a pattern reported by Brueggeman et al. [1987] in the southeastern Gulf of Alaska), and the whales are able to travel in relatively shallow (100-150 m) water off the north coast of

Washington as the continental shelf (water <200 m deep) here extends nearly 75 km from shore.

Our study also supports previous observations (Pike 1962, Braham 1984, Brueggeman et al. 1987) that the southbound migration in general occurs farther offshore than the northbound, and further suggests that the southbound migration corridor, in particular, could overlap potential offshore oil development areas.

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Literature Cited

- Andrews, R. C. 1914. Monographs of the Pacific Cetacea. I. The California Gray Whale (*Rhachainectes glaucus* Cope). Mem. Amer. Mus. Nat. Hist. n.s. 1:227-287.
- Braham, H. W. 1984. Distribution and migration of gray whales in Alaska. In M. L. Jones, S. L. Swartz, and S. Leatherwood (eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, New York. Pp. 249-266.
- Breiwick, J. M., D. J. Rugh, D. E. Withrow, M. E. Dahlheim, and S. T. Buckland. 1988. Preliminary population estimate of gray whales during the 1987/88 southward migration. Rep. Int. Whal. Comm., May 1988, San Diego. Unpubl.
- Brueggeman, J. J., G. A. Green, R. A. Grotefendt, and D. G. Chapman. 1987. Aerial surveys of endangered cetaceans and other marine mammals in the northwestern Gulf of Alaska and southeastern Bering Sea. Final Report for MMS/NOAA/OCSEAP, Anchorage, Contract No. 85-ABC-00093, Research Unit 673. 139 pp. plus appendices.
- Hatler, D. F. and J. D. Darling. 1974. Recent observations of the gray whale in British Columbia. Can. Field-Nat. 88:449-459.
- Herzing, D. L. and B. R. Mate. 1984. Gray whale migrations along the Oregon coast, 1978-1981. In M. L. Jones, S. L. Swartz, S. Leatherwood (eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, New York. Pp. 289-307.
- Hessing, P. 1981. Gray whale (*Eschrichtius robustus*) migration into the Bering Sea observed from Cape Sarichef, Unimak Island, Alaska, Spring 1981. Final Rep. Contract NA81SRGA 00080. Outer Continental Shelf Environmental Assessment Program, NOAA, Juneau. 28 pp.
- Howell, A. B. and L. M. Huey. 1930. Food of the gray and other whales. J. Mammal. 11:321-322.
- Hubbs, C. L. 1959. Natural history of the gray whale. Proc. XVth Int. Congress Zool. 159:313-316.
- Jones, M. L. and S. L. Swartz. 1987. Radio-telemetry study and aerial census of gray whales in the Channel Islands National Marine Sanctuary during the southward migration, January 1986. Final Rep. prepared for NWAFC/NMFS/NOAA, contract No. 50-ABNF-6-00067.
- Kent, D. B., S. Leatherwood, and L. Yohe. 1980. Responses of migrating gray whales, *Eschrichtius robustus*, to oil on the sea surface: Results of a field evaluation, Vol. I. Final Rep. from Hubbs-Sea World Research Institute to Univ. Guelph, Ontario. Contract No. P-0057621.
- Leatherwood, S. 1974. Aerial observations of migrating gray whales *Eschrichtius robustus*, off southern California, 1969-1972. Mar. Fish. Rev. 36:45-49.
- Neter, J. and W. Wasserman. 1974. Applied Linear Statistical Models. Richard D. Irwin, Inc., Homewood, IL. 842 pp.
- Pike, G. C. 1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish. Res. Bd. Can. 19:815-838.
- Poole, M. M. 1984. Migration corridors of gray whales along the central California coast, 1980-1982. In M. L. Jones, S. L. Swartz, S. Leatherwood (eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press, New York. Pp. 389-407.
- Rice, D. W. 1965. Offshore southward migration of gray whales off southern California. J. Mammal. 46:504-505.
- Rice, D. W. and A. A. Wolman. 1971. The Life History and Ecology of the Gray Whale (*Eschrichtius robustus*). Am. Soc. Mammal., Special Publ. No. 3.
- Rugh, D. J. 1984. Census of gray whales at Unimak Pass, Alaska: November-December 1977-1979. In M. L. Jones, S. L. Swartz, S. Leatherwood (eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press. New York. Pp. 225-248.
- Townsend, C. H. 1887. Present condition of the California gray whale fishery. Bull. U.S. Fish. Comm. 6:340-360.
- Wolman, A. A. 1985. Gray whale - *Eschrichtius robustus*. In S. H. Ridgway and R. Harrison (eds.), Handbook of Marine Mammals. Academic Press, London. Pp. 67-90.
- Wilke, F. and C. H. Fiscus. 1961. Gray whale observations. J. Mammal. 42:108-109.
- Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 pp.

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Enhancement Effects of Spawning Pink Salmon on Stream Rearing Juvenile Coho Salmon: Managing One Resource to Benefit Another

Abstract

This paper examines the relationship between the number and biomass of pink salmon spawning in the Skagit River and the resulting return of adult coho salmon which were rearing as age-0 fish in the watershed at the time of spawning. From 1967 through 1985, during the odd-numbered years, there is a strong direct correlation between the biomass of pink salmon spawners present in the Skagit River and recruit per spawner for coho salmon present in the system as age-0 fish at the time of pink salmon spawning. Moderate flows, or at least the lack of large freshets in October, increase the benefit that pink carcasses provide. Further, the streamflow in summer shows a strong positive influence on recruit per spawner for coho salmon. Traditional salmon management has concentrated on one species at a time. In order to take advantage of the enhancement benefit conferred by pink salmon spawners it will be necessary to examine interspecies impacts, reduced consumptive fisheries, changes in land use activities, and changes in stream flows from a much broader perspective than is presently employed.

Introduction

Anadromous salmonids native to the Pacific coast of North America, such as Pacific salmon, trout, and char are known for their intriguing life cycles. Adults spawn in gravel of freshwater lakes and streams. Depending on species, emerging young either migrate to saltwater within a short period of time (days or weeks) or spend up to four years in freshwater before migrating to saltwater (Groot and Margolis 1991). After one to six years at sea, adults return to their natal stream to spawn. Pacific salmon (*Oncorhynchus* spp.), are semelparous and die after spawning, whereas Pacific trout (formerly *Salmo* but now classified as *Oncorhynchus*) and char (*Salvelinus*) may be iteroparous and generally survive at least one spawning migration (Scott and Crossman 1973). Depending on species, juveniles will weigh between 0.13 grams (g) and 35g when they migrate to the ocean. The range in weight for returning adults, again depending on species, is between 0.5 kilogram (kg) and 45 kg (Groot and Margolis 1991).

Recently, attention has been focused on the declines of wild salmon populations in the Pacific Northwest (Nehlsen, et al. 1991; Palmisano, et al. 1993; Wissmar, et al. 1994; and McIntosh et al. 1994). Historically, the rivers and streams along the Pacific coast of North America supported vast numbers of spawning salmon. For example, the Fraser River in British Columbia produced sockeye salmon (*Oncorhynchus nerka*) runs of

between 30 and 40 million fish (Roos 1991, Gilhousen 1992). Ricker (1987) estimated some individual spawning streams in the Fraser River watershed may have had as many as 1 million spawning sockeye per kilometre (km) of river. Even today, some rivers such as the Fraser continue to have spawning escapements in the millions of fish (Roos 1991).

Large spawning aggregations of salmon transport significant amounts of nutrients from marine waters to freshwater systems. Kline et al. (1990), using isotopes of marine origin, documented that salmon carcasses provided a significant amount of the nutrients which "fed" streamlife. Richey et al. (1975) demonstrated that peaks of nutrient levels, carbon fixation, and periphyton biomass occurred following spawning and death of resident sockeye salmon (kokanee) in a stream. Koenings and Burkett (1987) suggested that fewer spawners, resulting in reductions in nutrient input, may be partially responsible for the inability of the sockeye salmon population to increase to historic levels in Karluk Lake, Alaska.

Salmon management has traditionally focused on a single species at a time. In this paper, the relationship among the numbers and biomass of spawning pink salmon (*O. gorbuscha*) and the numbers of adult coho salmon (*O. kisutch*) returning two years later was examined. The Skagit River system was chosen because the number of spawning pink salmon is relatively large when

compared to other salmon species in the system (hundreds of thousands versus tens of thousands) and the Skagit River coho salmon stock has been critical to fishery management in Washington State in recent years due to its generally low level of abundance throughout its migratory range. The argument is developed that management schemes which consider interspecies effects may be more beneficial to overall fish production from a given watershed, especially when the overall ecosystem impacts are considered. Also discussed are the impacts that management of terrestrial resources (such as land and timber management) may have on fish production and vice versa.

Pink salmon are the most abundant and smallest bodied Pacific salmon species (Heard 1991). In their native range, pink salmon have a fixed two-year life cycle. Skagit River pink salmon spawn in odd-numbered years, normally in September and October. Most of the spawning occurs in the mainstems of the Skagit River and its major tributaries. Following emergence from the gravel, the fry immediately migrate downstream to saltwater.

Coho salmon have a longer and more complex life cycle than do pink salmon; they typically live in fresh water for one or two years prior to their migration to the ocean as smolts. This migration typically occurs in the spring with peak movement occurring in May. Mature coho salmon return to fresh water to spawn after spending (approximately) six or eighteen months at sea (Sandercock 1991). In the Skagit River watershed most coho spawning occurs in small tributary streams.

Study Area and Methods

Although the headwaters of the Skagit River are in Canada, most of the drainage basin is located in the northwest portion of Washington State. The mainstem Skagit River, upstream from river km 144, has a series of hydroelectric dams which are blockages to upstream fish migration.

The number of fish (run size), number of spawners (escapement), and average weights used in the analyses came from Washington Department of Fish and Wildlife (WDFW) files. The total run sizes for Skagit River origin coho salmon and pink salmon are the estimated numbers of spawners plus an estimate of catch taken by commercial net fisheries in Puget Sound. WDFW as-

sumed the number of salmon calculated in the estimates of run sizes consistently reflected stock abundance (Washington Dept. of Fisheries 1984).

The escapement estimates for both species of salmon were based on visual counts of live and dead fish in selected sections of spawning streams (index areas). Surveys are conducted on a regular schedule, water conditions permitting, during the spawning seasons. The counts from the index areas are expanded based on relationships developed in "base years" between the index counts and total system escapement (G. Zillges and J. Ames, WDFW biologists, pers. comm.).

Recruit per spawner (R/S) is defined as the number of returning adult fish (recruits) produced from a given number of spawners. An R/S less than 1.00 means each parent produced less than one surviving offspring. Ultimately, this rate of reproduction leads to extinction. Conversely, an R/S greater than 1.00 means each parent produced more than one surviving offspring. For fish resources managed for consumptive harvest, recruits in excess of the desired number of spawners are available for harvest.

Total biomass of pink salmon carcasses per year was calculated by multiplying the number of spawning pink salmon by the mean weight of pink salmon caught in Puget Sound at Skagit Bay and in the Skagit River by commercial fishermen. In order to account for differential availability of salmon carcasses due to stream flows (per Hunt et al. 1992) the biomass of pink salmon carcasses was adjusted by multiplying the carcass biomass by the inverse ratio of flow in October (mean or peak) in that year to the overall mean flow (mean or peak) for all years. The effect of this adjustment is to increase the "carcass biomass" in years of lower than average flows and decrease it for years when flows were greater than the mean.

The Puget Sound Index (PSI) is a measure of summer low flows from a representative group of streams which discharge into Puget Sound. Low stream flows are often used to predict adult coho salmon abundance because of the inverse relationship between summer flow levels during juvenile rearing and adult coho returns (Mathews and Olson 1980). Streamflow data are taken from United States Geological Survey files.

Pink salmon spawning escapement, carcass biomass (including adjusted biomass), coho spawning escapement, PSI, and Skagit River flows in

October were regressed against coho R/S. Variables were regressed singly and in stepwise fashion to determine correlations.

Results and Discussion

During odd-numbered years between 1967 and 1985, WDFW estimated that between 100,000 and 710,000 pink salmon spawned per year in the Skagit River, resulting in carcass deposition of an estimated 213,000 to 1,642,000 kg (Table 1). The R/S for coho rearing in the system at the time of pink spawning during these years ranged between 0.677 and 3.479, with higher R/S values associated with the larger pink salmon escapements (Table 1).

There is a positive correlation between biomass of pink salmon carcasses and coho salmon R/S. Biomass of pink salmon carcasses indexed to reflect peak and mean October flows showed strong correlations ($r^2=.762$, $p<.001$ and $r^2=.656$, $p=.005$, respectively) with coho R/S salmon (Table 2). Coho salmon recruit per spawner was also significantly correlated with coho spawning escapement and the peak river flow in October ($r^2=.428$, $p=.040$ and $r^2=.402$, $p=.049$, respectively) (Table 2). Stepwise regression utilizing all variables regressed against coho salmon R/S added the PSI to pink salmon biomass indexed for peak October flow. The resulting regression with coho salmon

R/S increased the r^2 to 0.895 and $p<=.001$ (Table 2).

Return of adult coho salmon, expressed as a ratio of returning adults to numbers of spawners, shows a strong positive correlation with the biomass of pink salmon which spawned while the coho salmon juveniles were rearing in the river. As the amount of pink salmon carcass biomass entrained in the Skagit River system increased, the number of coho salmon adults per spawner increased. It was assumed that pink salmon carcass entrainment was inversely correlated with streamflow; this was supported by the increased correlations when carcass biomass was indexed to reflect October flow conditions. Summer low flow, as measured by the PSI, shows a direct relationship between adult coho produced from the Skagit River system with lower summer flows resulting in fewer adult fish.

Based on the correlations calculated in this study, observations of other streams, and a review of the literature, I offer the following as the enhancement mechanism.

During spawning, pink salmon disturb large areas of stream bottom. The more spawners that are present, the greater the disturbed area. Physical disturbance displaces the insects living on the bottom and causes them to drift downstream where they can be eaten by fish. Field-Dodgson (1987)

TABLE 1. Pink salmon and coho salmon run size and carcass biomass and Skagit River flows, 1967-1985.

Year	Pink		Coho		Puget Sound Index	*Skagit River Flow		Adjusted Carcass Biomass	
	Escapement Number	Kilogrammes (kg)	Escapement Number	R/S		Peak cms	Mean cms	Peak Flow (kg)	Mean Flow (kg)
1967	100000	235000	25500	0.677	6.602	1755	351	123000	197000
1969	100000	254000	21000	1.244	8.477	733	378	318000	197000
1971	300000	694000	21800	1.240	9.370	521	250	1222000	816000
1973	250000	624000	19800	1.263	6.512	708	249	808000	735000
1975	100000	1290000	31800	1.400	12.274	1480	170	180000	501000
1977	500000	1338000	16000	3.442	8.385	357	198	3440000	1982000
1979	300000	680000	14100	1.521	6.610	614	230	1015000	870000
1981	100000	213000	25500	1.375	8.821	931	408	210000	153000
1983	470000	938000	9000	3.479	12.765	422	218	2039000	1266000
1985	710000	1642000	35600	1.169	7.513	1647	485	914000	994000
Mean	293000	690800	22010	1.681	8.733	917	294	1026900	771100

*Data from site 1200500, near Mt. Vernon, Washington

TABLE 2. Single and stepwise regression analyses for selected variables.

Variables	df	r-sq	F-value	p
Single regressions				
pink kg-adj peak	8	0.762	25.55	<<0.001
pink kg-adj mean	8	0.656	15.26	0.005
coho escapement	8	0.428	5.99	0.040
peak flow	8	0.402	5.38	0.049
mean flow	8	0.246	2.60	0.145
Puget Sound Index (PSI)	8	0.239	2.52	0.151
pink escapement	8	0.229	2.38	0.162
pink kilograms	8	0.227	2.35	0.164
Stepwise regression				
adj kg-peak, PSI	7	0.895	29.84	<<0.001

documented that spawning chinook salmon (*O. tshawytscha*) were able to depopulate a stream of its insect population. Further, the level of depopulation was directly related to the number of spawners. Spawners also dig up previously spawned eggs making them available to fish. Following spawning, the salmon die. Coho juveniles are then able to feed on the decomposing carcasses (R. Bilby, Weyerhaeuser Aquatic Ecologist, pers. comm.).

As the carcasses decompose, they are incorporated into the stream food web (R. Bilby, Weyerhaeuser Aquatic Ecologist, pers. comm.). The captured energy is then cycled through the system and becomes available to the coho, primarily as insects. Many of the carcasses are hauled out of the stream onto land for consumption by terrestrial animals and subsequent nutrient cycling through the terrestrial ecosystem (Cederholm, et al. 1989). Some of the energy captured in the terrestrial systems may return to the river and be added to the food resources available to coho. Johnston et al. (1990) showed applications of fertilizer to a coastal river in British Columbia substantially increased the average weight of juvenile salmonids. Andersen et al. (1992) showed growth rates for age 0 brown trout (*S. trutta*) were directly related to food resources available to the fish. The fish in the stream with the greatest food supply were both faster growing and larger at the end of the experiments. Other studies have documented survival to adulthood for coho salmon smolts increases with increasing size of out-migrant (Holtby et al. 1990). Bilby and Bisson (1992) believe increasing nutrients in streams might be

beneficial to juvenile anadromous fish production by increasing the amount of food available.

Increasing the biomass of pink salmon carcasses entrained in the Skagit River system can be accomplished in a number of ways, including allowing more pinks to spawn, utilizing dams to have better control of both maximum and minimum flows, or increasing the ability of the river to trap and hold the carcasses. These, as well as other options, can be combined into a holistic package of management options for the system.

Increasing the numbers of pink salmon spawning in the Skagit River, however, may have a negative impact on the production of chum salmon. Ames (1983) estimated that an increase in Puget Sound pink salmon spawning escapement from 300,000 to 900,000 would reduce R/S for all Puget Sound chum salmon from 3.25 to 1.45. He surmised that there was competition for food between pink and chum salmon fry with the pink salmon being able to outcompete the chum salmon. The interactions between chum, coho, and pink salmon and the impact of escapement changes on other species of salmonids which rear in the Skagit system, such as chinook salmon, steelhead trout (*O. mykiss*), cutthroat trout (*O. clarki*), Dolly Varden (*S. malma*), and bull trout (*S. confluentus*), may also reveal similar interconnections.

In addition to the potential loss of chum salmon production, an increase of pink salmon escapement in the Skagit River could require at least a short-term reduction of harvest of Skagit River pink salmon in years of low runsizes. The reduction in catch would primarily affect the commercial

net fishermen operating in Skagit Bay and the Skagit River. The loss in catch would reduce their incomes. The benefits in coho salmon production would generally accrue to the marine hook and line fleets, although an increase in coho abundance would provide additional harvest by bay and river fishermen. Also, the coho salmon hook and line and the pink salmon net fisheries are generally geographically separate, so different communities would benefit.

Entrainment of salmon carcasses requires that there be a certain level of complexity in the stream environment. Recent studies have shown that habitat complexity, as measured by the amount of debris and rock in a channel, increases the ability of a stream to retain and cycle nutrients (Cederholm and Peterson 1985, Sedell et al. 1988, Dobson et al. 1992, Garman et al. 1992). Growns and Davis (1991) showed that eight years after logging there were still significant differences in the invertebrate communities between clearcut and unlogged areas. They further found that invertebrate communities in a stream which had been protected by a 100 m-wide buffer strip had a different community structure than that found in the unlogged streams. But the communities in the stream protected by the buffers were more similar to the unlogged streams than to streams in the clearcut areas. By retaining or enhancing a stream's ability to capture, retain, and cycle nutrients more energy will be present in the system and available to the fish living there.

An objective evaluation of any change in resource management, such as increasing the pink salmon escapement to increase adult coho salmon return is difficult. While the value of a resource which has a commercial market value is relatively easy to calculate, it is difficult to calculate the "value" of a resource which has recreational harvest values, recreational non-harvest values, "spiritual" values, and ecosystem values independent of commercial harvest. The problem becomes even more complex when land use questions, growth management issues, and industries such as logging and agriculture must be considered.

The problem becomes even further exacerbated by a political system which views planning as "what will we do tomorrow?" and long range planning as "the next budget cycle." The research necessary to actually understand the interrelation-

ships of the components of an ecosystem is expensive and time-consuming. Anyone familiar with the fiscal climate in recent years knows that government finds it difficult to address future benefits. Consequently, we deal with today's problems today and tomorrow's problems at some other time.

Summary

There is a strong direct correlation between the biomass of pink salmon spawners present in the Skagit River and recruit per spawner for coho salmon present in the system as age-0 fish at the time of pink salmon spawning. It appears that moderate flows, or at least the lack of large freshets in October, increase the benefit that pink carcasses provide. Further, the streamflow in summer shows a strong positive influence on recruit per spawner for coho salmon.

Based on the relationship between pink salmon and coho salmon, and the potential for interactions with other salmonid species, it is obvious that decisions regarding spawner escapement levels for one species need to consider the impacts on, and interactions with, other species. There may be instances when it is more valuable to long term productivity of an ecosystem and overall societal economic benefit to forego catch of one species in order to increase the abundance of another. There is a need to further study the relationship between nutrient level in streams and resultant fish populations. Finally, the relationships between fish production and development in a basin needs to be evaluated so resource management and utilization decisions can be made which will integrate the entire ecosystem rather than isolate each piece with decisions made in a vacuum.

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Literature Cited

- Ames, J. J. 1983. Salmon stock interactions in Puget Sound: a preliminary look. In M. A. Miller. Southeast Alaska coho salmon research and management review and planning workshop. ADFG Rept. Pp.84-95.
- Andersen, T. H., H. O. Hansen, T. M. Iversen, D. Jacobsen, L. Krojgaard, and N. Poulsen. 1992. Growth and feeding of 0+ brown trout (*Salmo trutta* L.) introduced to two small Danish streams. Arch.Hydrobiol.125:339-346.
- Bilby, R. E. and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. 49:540-551.
- Cederholm, C. J. and N. P. Peterson. 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. Can. J. Fish. Aquat. Sci.42:1222-1225.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Can. J. Fish. Aquat. Sci. 46:1347-1355.
- Dobson, M., A. G. Hildrew, A. Ibbotson, and J. Garthwaite. 1992. Enhancing litter retention in streams: do altered hydraulics and habitat confound field experiments? Freshwater Biology 28:71-79.
- Field-Dodgson, M. S. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. Hydrobiologia. 154:3-11.
- Garman, G. C. 1992. Fate and potential significance of postspawning fish carcasses in an Atlantic coastal river. Trans. Amer. Fish. Soc. 121:390-394.
- Gilhousen, P. 1992. Estimation of Fraser River sockeye escapements from commercial harvest data, 1892-1944. Int. Pac. Sal. Fish. Comm. Bull 27. 114 p.
- Groot, C. and L. Margolis, eds. 1991. Pacific salmon life histories. UBC Press, Vancouver. 564 p.
- Growns, I. O. and J. A. Davis. 1991. Comparison of the macroinvertebrate communities in streams in logged and undisturbed catchments 8 years after harvesting. Aust. J. Mar. Freshwater Res. 42:689-706.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus kisutch*). In Groot, C. and L. Margolis, eds. Pacific salmon life histories. UBC Press, Vancouver. Pp.119-230.
- Holtby, L. B., B. C. Anderson, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47:2181-2194.
- Hunt, W. G., B. S. Johnson, and R. E. Jackman. 1992. Carrying capacity for Bald Eagles wintering along a north-western river. Raptor Res. Jour. 26:49-60.
- Johnston, N. T., C. J. Perrin, P. A. Slaney, and B. R. Ward. 1990. Increased juvenile salmonid growth by whole-river fertilization. Can. J. Fish. Aquat. Sci. 47:862-872.
- Kline, T. C., Jr., J. J. Goering, O. A. Mathisen, P. H. Poe, and P. L. Parker. 1990. Recycling of elements upstream by runs of Pacific salmon: I. d15N and d13C evidence in Sashin Creek, southeastern Alaska. Can. J. Fish. Aquat. Sci. 47:136-144.
- Koenings, J. P. and R. D. Burkett. 1987. An aquatic Rubic's cube: restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*). In H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci.96. Pp. 419-434.
- Mathews, S. B. and F. W. Olson. 1980. Factors affecting Puget Sound coho salmon (*Oncorhynchus kisutch*) runs. Can. J. Fish. Aquat. Sci. 37:1373-1378.
- McIntosh, B. A., J. R. Sedell, J. E. Smith, R. C. Wissmar, S. E. Clarke, G. H. Reeves, and L. A. Brown. 1994. Historical changes in fish habitat for select river basins of eastern Oregon and Washington. NW Sci. 68:36-53.
- Nehlsen, W., J. E. Williams, and J. A. Lichtowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4-21.
- Palmisano, J. F., R. H. Ellis, and V. W. Kaczynski. 1993. The impact of environmental and management factors on Washington's anadromous salmon and trout, summary and recommendations. Wash. For. Prot. Assoc. and Wash. Dept. Nat. Res. Olympia. p. 54.
- Richey, J. E., M. A. Perkins, and C. R. Goldman. 1975. Effects of kokanee salmon decomposition on the ecology of a subalpine stream. J. Fish. Res. Bd. Can. 32:817-820.
- Ricker, W. E. 1987. Effects of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rept.Fish. Aquat. Sci. 1522. 75 p.
- Roos, J. F. 1991. Restoring Fraser River salmon. Pac. Sal. Comm. Vanc. B.C. 448 p.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In Groot, C. and L. Margolis, eds. Pacific salmon life histories. UBC Press, Vancouver. Pp.395-446.
- Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184, Fish. Res. Bd. Can., Ottawa. 966 p.
- Sedell, J. R., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers. In C. Masur, R. F. Tarrant, J. M. Trappe, and J. F. Franklin (eds.) From the forest to the sea: A story of fallen trees. U.S. Dept. Agr. Gen. Tech. Rept. PNW-GTR-229. Pp. 47-81.
- Washington Department of Fisheries. 1984. Strategic plan for managing Washington salmon stocks, Washington salmon stock inventory appendices G-I. Wash. Dept. Fish. Olympia. 428 p.
- Wissmar, R. C., J. E. Smith, B. A. McIntosh, H. W. Li, G. H. Reeves, and J. R. Sedell. 1994. A history of resource use and disturbance in riverine basins of western Oregon and Washington (early 1800s-1990s). NW Sci. 68:1-35.

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 1500 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect, Macintosh or DOS), to the Editor.

R. Lee Lyman, Department of Anthropology, University of Missouri, Columbia, Missouri 65211

Inaccurate Data and the Olympic National Park Mountain Goat Controversy

Introduction

About a dozen mountain goats (*Oreamnos americanus*) were released in the Olympic Mountains of western Washington in the 1920s (Moorhead and Stevens 1982). The fate of the descendants of these goats has recently become controversial (Scheffer 1993; Lyman 1994). Olympic National Park (ONP)—which now administers the land occupied by the goats—seeks to eradicate the population (National Park Service [NPS] 1995). Eradication is justified by scientific research that has “undergone thorough academic scrutiny [and] peer review” (Crawford 1993:15). It is, however, very easy to discover errors in that research. I focus here on one example of this, and briefly mention two others.

The purpose of a monograph titled “Mountain Goats in Olympic National Park” and published in late 1994 by the NPS is stated in the introduction: “Mountain goat management at Olympic National Park has been controversial. No matter how the issue is eventually resolved, the decision must be based, in part, on scientific information. We trust that this monograph provides the information necessary” (Houston and Schreiner 1994:12). Thus, data summarized in the

monograph are viewed by ONP personnel as critical to resolution of the controversy. Here, I document errors in the mammalian data presented in Chapter 3, “Biogeography of the Olympic Peninsula” (Houston et al. 1994), and illustrate how those errors might prompt a reader to conclude that the preferred wildlife-management decision should be to eliminate the extant mountain goats from ONP.

Rules and Missing Mammals

Biologists working on ONP—including Houston et al. (1994:34)—typically mention mammal species missing from the park but found in the Cascade Mountains of Washington (Table 1) as evidence that mountain goats were never present in the former area (e.g., Moorhead and Stevens 1982). However, the twelve species Houston et al. list do not have the same biogeographic access to the Olympics. One—the northern bog lemming, (*Synaptomys borealis*)—is today rarely found only in the extreme northernmost Cascades of Washington (Wilson et al. 1980), thus it should not be included with the other species as nearly all of them are today found in the southern Cascades (e.g., around Mount Rainier). By relaxing the

TABLE 1. Lists of mammal species historically absent from the Olympic Peninsula.^a

species	Scheffer 1949	Johnson and Johnson 1952	Moorhead and Stevens 1982	Houston et al. 1994
<i>Ochotona princeps</i>	+	+	+	+
<i>Spermophilus saturatus</i>	+	+	+	+
<i>Microtus richardsoni</i>	+			+
<i>Synaptomys borealis</i>	+			+
<i>Erethizon dorsatum</i>	+			+
<i>Canis latrans</i>	+			+
<i>Vulpes vulpes</i>	+	+		+
<i>Ursus arctos</i>	+	+		+
<i>Gulo luscus</i>	+			+
<i>Lynx canadensis</i>	+	+		+
<i>Oreamnos americanus</i>	+	+	+	+
<i>Ovis canadensis</i>	+		+	+

^aSpecies indicated by “+” are listed by author(s) heading the column as species not found in the Olympics but historically present in the Cascades of Washington.

criteria for inclusion of species in their list of missing mammals, and therefore including the northern bog lemming and other taxa, Houston et al. (1994) effectively double the length of the only list compiled by a non-park biologist (Johnson and Johnson 1952). The difference here probably resides in varied rules for defining the set of “missing mammals.” Houston et al. (1994) specify no rules, and this leads to inaccurate data.

Insular Faunas and Missing Mammals

Houston et al. (1994:37) compare the presence-absence of mammalian species on the Olympic Peninsula to the presence-absence of mammals on Vancouver Island, the Queen Charlotte Islands, and the Alexander Archipelago. They point out that “In common with the Olympic Peninsula, [these] landbridge islands have impoverished faunas compared to the adjacent mainland” (Houston et al. 1994:43-44). They continue:

Mammals missing from the landbridge island faunas include species that were absent historically from the Olympics as well—the mountain goat included. As with the Olympics, the mammal absences mean either that the species failed to colonize because of environmental barriers or that earlier populations met extinction.

Apparently, because the lists of mammals missing from the islands are similar, and because those lists are also similar to the list of mammals miss-

ing from the Olympics, those same mammals probably never colonized the islands or the Olympics. This is so because “No obvious characteristics or relations have been identified that are common among species absent from the peninsula and from the landbridge islands that would similarly predispose populations to extinction” (Houston et al. 1994:45). The critical point, then, is the similarity of the lists.

Houston et al. (1994:43) state that various islands of the Alexander Archipelago lack 18 species. Several of the species they list as today missing from archipelago are, however, present there. Their list indicates that the hoary marmot (*Marmota caligata*), northern redback vole (*Clethrionomys rutilus*), muskrat (*Ondatra zibethicus*), jumping mouse (*Zapus hudsonius*), porcupine (*Erethizon dorsatum*), wolverine (*Gulo luscus*), moose (*Alces alces*), and mountain goat are not found on any of the islands of the Alexander Archipelago. Reviewing the literature they cite (Cowan and Guiguet 1965; Manville and Young 1965), plus an additional reference (Swarth 1936), I find all of the species listed in the preceding sentence to occur on one or more of the islands of the archipelago. Omitting from Houston et al.’s list those incorrectly listed species, the Alexander Archipelago is not impoverished by 18 species but rather by only 6. The latter include the northern water shrew

TABLE 2. Mammals historically missing from Vancouver Island.

Species listed by Houston et al. 1994	Cowan and Guiguet 1965 ^a	Banfield 1974 ^a
<i>Sorex cinereus</i>	46	10
<i>Scapanus orarius</i>	—	31
<i>Ochotona princeps</i>	94	74
<i>Lepus americanus</i>	103	84
<i>Apodonta rufa</i>	—	95
<i>Eutamias amoenus</i>	141	104
<i>Glaucomys sabrinus</i>	159	146
<i>Neotoma cinerea</i>	193	177
<i>Synaptomys borealis</i>	197	190
<i>Clethrionomys gapperi</i>	204	183
<i>Microtus longicaudus</i>	226	217
<i>Ondatra zibethicus</i>	231	200
<i>Erethizon dorsatum</i>	—	236
<i>Canis latrans</i>	279	288
<i>Vulpes vulpes</i>	288	300
<i>Ursus arctos</i>	—	310
<i>Martes pennanti</i>	308	319
<i>Spilogale gracilis</i>	—	338
<i>Mephitis mephitis</i>	—	340
<i>Lynx rufus</i>	341	353
<i>Oreamnos americanus</i>	391	410
Species not listed by Houston et al.		
<i>Sorex bendirii</i>	55	15
<i>Sorex trowbridgii</i>	—	19
<i>Neurotrichus gibbsii</i>	—	28
<i>Scapanus townsendii</i>	—	29
<i>Eutamias townsendii</i>	144	105
<i>Clethrionomys occidentalis</i>	204	179
<i>Phenacomys intermedius</i>	201	192
<i>Microtus oregoni</i>	215	221
<i>Zapus trinotatus</i>	243	225
<i>Mustela frenata</i>	318	324

^aNumbers in these columns are the page number on which the range map for the species is shown by the indicated author; if —, no map is shown and only verbal descriptions of the range are provided.

(*Sorex palustris*), collared pika (*Ochotona collaris*), showshoe hare (*Lepus americanus*), lynx (*Lynx canadensis*), coyote (*Canis latrans*), and red fox (*Vulpes vulpes*).

Houston et al. (1994:43) state that Vancouver Island lacks 19 species of mammals found on the mainland but list 21. Their data are summarized in Table 2, along with additional information. I consulted the same reference that Houston et al. did (Cowan and Guiguet 1965), plus two more recent titles (Banfield 1974; Nagorsen 1990). I found that at least ten additional species of mammals not listed by Houston et al.—but all listed in the single reference they cite—should be included in the list of mammals missing from Vancouver Island. If all species that occupied any fraction of the mainland coast adjacent to Vancouver Island are included, then the list of mammals missing from the island is not 19 or 21 species, rather it is the total 31 species listed here in Table 2.

If the errors are ignored, the lists of mammals absent from Vancouver Island, the Alexander Archipelago, and the Olympics appear similar; if those errors are corrected, then those lists are not very similar. Here I use the Sorenson Index to show how these errors make Houston et al.'s lists look more similar than the correct lists. The Sorenson Index is calculated with the formula

$$[2C/(A + B)] 100 = S$$

where C is the number of species held in common by the two compared species lists, A is the total number of species in one of the lists, B is the total number of species in the other list, and S is the index value. The Sorenson index, or S, is similar to a measure of the percentage of all the species found in two lists that are shared by the two lists.

Data used in the calculations are presented in Tables 1 and 2 and in the text above on the Alexander Archipelago. Houston et al. indicate the Olympics are missing 12 species, Vancouver Island is missing 21, and the Alexander Archipelago is missing 18. The number of species shared by each possible pair of lists is 9 for Vancouver Island and the Alexander Archipelago, 7 for the Alexander Archipelago and the Olympics, and 8 for Vancouver Island and the Olympics. The S values for each possible pair of biogeographic islands are:

Alexander Archipelago	46	
Olympic Mountains	48	47
Vancouver Island		Alexander Archipelago

The S values indicate that about half of the missing species are found in each pair of lists; thus the lists of missing mammals produced by Houston et al. appear similar.

If we use the corrected lists—as I have described them—of missing mammals, Vancouver Island has 31 missing species (Table 2), the Alexander Archipelago is missing 6 (only species missing from all islands of the archipelago are included), and the Olympics are missing 11 (northern bog lemming omitted). The lists of missing mammals for Vancouver Island and the Alexander Archipelago share 4 species, the Alexander Archipelago and the Olympics lists share 3 species, and the Vancouver Island and the Olympics lists share 7 species. The S values calculated using these numbers are:

Alexander Archipelago	22	
Olympic Mountains	33	35
Vancouver Island		Alexander Archipelago

These S values are 12 to 24 points less (they drop 25 to 52%) than those derived using Houston et al.'s lists. The greatest proportion of missing mammals of any one pair is only 35 percent.

Comparison of the S values calculated using the corrected lists of missing mammals with those calculated using Houston et al.'s lists show how the inaccuracies in the latter enhance their similarities. Perhaps the errors crept into Houston et al. (1994) simply because mistakes happen. But if one wishes to argue that the Olympic Mountains were never colonized by a certain set of mammal species—including mountain goats—then one strategy would be to show that most members of that set of species failed to colonize other, similar geographic places. Which ever is the case, while Houston et al. consulted several mammalogists familiar with Vancouver Island (e.g., D. Nagorsen), they failed to read Banfield's (1974) book and they did not read Cowan and Guiguet's (1965) book very closely (they consistently misspell the second author's name).

Twenty-three scientists read a draft of the chapter (Houston et al. 1994:210) prior to its publication, but none detected the errors described above

(the published version is similar to a draft that nine reviewers saw). Nine of those scientists were paid for their efforts by NPS, but they were only given three weeks to complete their reviews of Houston et al.'s paper, along with three other documents. Thus, maybe these nine reviewers did not have the time to read and study the relevant *primary* literature. Of course, had any of these nine reviewers been experts in mammalian biogeography or the mammalogy of the Pacific Northwest, one of them should have detected some of the errors. Instead, one of the nine paid reviewers (an historian) found the argument and the data on mammals missing from the Olympics, Vancouver Island, and the Alexander Archipelago to be "compelling evidence" that mountain goats never occupied the Olympics; another of the nine (an historian) found this same inaccurate data to argue "very strongly" for the failure to colonize hypothesis (unpublished documents on file, ONP, Port Angeles, Washington).

Ignorance is Bliss, and Advantageous

I informed then ONP Superintendent Maureen Finnerty that factual errors were contained in a draft of Houston et al. (1994) and offered to describe those errors in letters dated May 19, 1994, and August 25, 1994. While I received responses to these letters from ONP, my offer was ignored. The monograph in which Houston et al. (1994) is found was shipped from the printers in Salt Lake City to the Denver distribution center on January 13, 1995 (NPS Publications Coordinator, Denver, personal communication to Lyman, Jan. 20, 1995). Was it, then, too late to make corrections to the manuscript in May 1994? It was not (D. B. Houston letter to Lyman dated March 9, 1995). Because the implications of the data found in Houston et al. (1994) are explicitly meant to have a direct bearing on the resolution of the Olympic mountain-goat controversy, it is important to document errors in the data in order to avoid uncritical acceptance of the flawed implications. Remaining ignorant of them would, of course, make the management decision ONP prefers—elimination of the extant mountain goats (NPS 1995)—a pill much more easily swallowed (Houston and Schreiner 1994:11-12).

I have become increasingly skeptical of the research produced by ONP scientists. It is, for example, easy to demonstrate that ONP resource

management specialist Paul Crawford's (1993:15) statement that "A thorough search of historical and archeological records has been conducted to answer any lingering doubts about the exotic status of the goats" is false. The ONP-sponsored review of the archaeological record was not thorough; 10 of the 34 total sites studied on the Olympic Peninsula are not mentioned (Lyman 1995). Further, the ONP historian (Schultz 1994) failed to mention Fannin and Grinnell's (1890:62) report that mountain goats "are found in considerable numbers on the high mountains west of Puget Sound...They are abundant on the Olympian Range

mountains." I thus urge interested scientists to critically examine all data relevant to the resolution of the ONP mountain goat controversy. Extermination of the mountain goats in Olympic National Park would, after all, be an irreversible management action. Just as Houston and Schreiner (1994) hope that their monograph helps, it is my hope that this paper will help with making the best-informed management decision.

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Literature Cited

- Banfield, A. W. F. 1974. *The Mammals of Canada*. National Mus. of Canada, Univ. of Toronto Press, Toronto.
- Cowan, I. McT. and C. J. Guiguet. 1965. *The Mammals of British Columbia*. British Columbia Provincial Museum Handbook 11.
- Crawford, P. 1993. Olympic mountain goat update. *Park Sci.* 13(3):15.
- Fannin, J. and G. B. Grinnell. 1890. Range of the white goat. *Forest and Stream* 34:62-64.
- Houston, D. B. and E. G. Schreiner. 1994. Introduction. In D. B. Houston, E. G. Schreiner, and B. B. Moorhead, eds. *Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species*. USDI Scientific Monograph NPS/NROLYM/NRSM-94/25. Pp. 5-12.
- Houston, D. B., E. G. Schreiner, and N. M. Buckingham. 1994. Biogeography of the Olympic Peninsula. In D. B. Houston, E. G. Schreiner, and B. B. Moorhead, eds. *Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species*. USDI Scientific Monograph NPS/NROLYM/NRSM-94/25. Pp. 28-46.
- Johnson, M. L. and S. Johnson. 1952. Check list of mammals of the Olympic Peninsula. *The Murrelet* 33:32-37.
- Lyman, R. L. 1994. The Olympic Mountain goat controversy: a different perspective. *Cons. Biol.* 8:898-901.
- Lyman, R. L. 1995. Determining when rare (zoo)archaeological phenomena are truly absent. *J. Archaeol. Method and Theory* 2. in press.
- Manville, R. H. and S. P. Young. 1965. *Distribution of Alaskan Mammals*. U.S.D.I. Bureau of Sports Fisheries and Wildlife Circular 221.
- Moorhead, B. B. and V. Stevens. 1982. Introduction and dispersal of mountain goats in Olympic National Park. In E. E. Starkey, J. F. Franklin, and J. W. Matthews, eds. *Ecological Research in National Parks of the Pacific Northwest*. Forest Research Laboratory, Oregon State Univ., Corvallis. Pp. 46-50.
- Nagorsen, D. 1990. *The Mammals of British Columbia: Taxonomic Catalogue*. Royal British Columbia Museum Memoir 4. Victoria.
- National Park Service. 1995. *Goats in Olympic National Park: Draft Environmental Impact Statement for Mountain Goat Management*. U.S.D.I., N.P.S.
- Scheffer, V. B. 1949. *Mammals of the Olympic Peninsula*, Washington. unpublished report on file, Olympic National Park, Port Angeles, Washington.
- Scheffer, V. B. 1993. The Olympic Mountain goat controversy: a perspective. *Cons. Biol.* 7:916-919.
- Schultz, S. 1994. Review of the historical evidence relating to mountain goats in the Olympic Mountains before 1925. In D. B. Houston, E. G. Schreiner, and B. B. Moorhead, eds. *Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species*. USDI Scientific Monograph NPS/NROLYM/NRSM-94/25. Pp. 256-293.
- Swarth, H. S. 1936. Origins of the fauna of the Sitkan District, Alaska. *Proc. Calif. Acad. Sciences, Fourth Series*, 23(3):59-78.
- Wilson, C., R. E. Johnson, and J. D. Reichel. 1980. New records for the northern bog lemming in Washington. *The Murrelet* 61:104-106.

Response to "Inaccurate Data and the Olympic National Park Mountain Goat Controversy"

Dr. R. Lee Lyman has had a long-standing interest in the mountain goat (*Oreamnos americanus*) management issue at Olympic National Park (Lyman 1988). Lyman (1995) contends that our recent monograph (Houston et al. 1994) contains errors in mammalian biogeography. For the most part, these perceived "errors" result from differing interpretations.

With respect to mammal occurrence, we noted 12 species of terrestrial mammals absent historically from the Olympic Mountains compared to the Cascades, based on the reports of 5 earlier workers. Lyman (1995) rules it inappropriate to include the bog lemming (*Synaptomys borealis*) in the list of absent mammals because the current range of the species does not extend far enough south. Fine, although Dalquest (1948:338) reports that the species "...was evidently forced southward by the Pleistocene glaciers into Washington and is now retreating northward in the wake of the ice."

Lyman disagrees with our list of 18 mammals reported missing from the Alexander Archipelago, and reports only 6 missing from the entire area. As reported in the text (Houston et al. 1994:43), "[t]he situation on Alaska's Alexander Archipelago is more complex, but up to 18 species are absent from one or more of the islands compared to the mainland"; this seems to be the major difference in interpretation. This meaning is not clear in the monograph table (p. 44) listing the species.

Lyman reports 31 species of mammals missing from Vancouver Island compared to the mainland, 10 more than we report. The main difference seems to be that I did not include species whose current ranges in British Columbia were limited to the southwestern tip of the mainland, i.e., their ranges did not extend far north along the mainland coast parallel to Vancouver Island (the range of *Phenacomys intermedius* does extend about one-third the distance). At least seven of these species are members of Dalquest's (1948)

Pacific Coastal Fauna that "...reaches its northern limit of distribution in Washington and is better represented farther south" (Dalquest 1948:52). Clearly, I should have explained the rationale for not including these species (Houston's variant of Lyman's bog lemming rule). In retrospect, the 10 species could be included on a list of mammals considered to be absent from Vancouver Island.

Our main point (Houston et al. 1994) is that terrestrial mammals and plants on the Olympic Peninsula share certain biogeographic characteristics with Vancouver Island, the Queen Charlotte Islands, and the Alexander Archipelago. The four areas support endemic forms of mammals and plants and have mammalian faunas that are comparatively impoverished. We expect these general patterns of species diversity and endemism to be reinforced as the biogeography of many groups of invertebrates is better understood.

With respect to the Fannin and Grinnell (1890) article on mountain goat distribution that so exercises Lyman (1995), Schultz simply overlooked it in her search through many hundreds of documents (S. Schultz, personal communication, May 1995). Fannin and Grinnell (1890) report that goats occurred in the Olympic mountains during the 19th century, but there is a mountain of evidence to the contrary (Schultz 1994). Fannin and Grinnell (1890) got it wrong in this early popularized account, just as they did other important points. They mistakenly reported that the historic range of the mountain goat included Colorado, as well as the southern Sierra Nevada of California. They also placed Mount Saint Helens and Mount Adams—with their goat populations—in Oregon instead of Washington.

Lyman (1988, 1994) has long disagreed with the National Park Service on mountain goat management, particularly interpretations of the archeological and historical evidence concerning the occurrence of mountain goats in the Olympic Mountains. Lyman reported that mountain goats

could have been present historically in the Olympic Mountains, but "...might not have been recorded because appropriate areas were not surveyed (Lyman 1988:14). As noted by Schultz (1994), considerably more historical information existed on early conditions in the Olympic Mountains than reported by Lyman (1988). Curiously, in subsequent reference to the 1988 paper Lyman claims that "...it was never my intent to review all of that [historical] information; I was more intent on figuring out a way to get goats into the Olympics" (Lyman to Houston, letter of 27 February 1995). Little seems to have changed.

I too encourage those interested to review the available documents, including Lyman's 1988

paper, Schalk's (1993) interpretation of the archeological/ethnographic information, and the Schultz (1994) review of the historic accounts of mountain goats on the Olympic Peninsula. Summaries of the nine independent reviews of these issues, so disparaged by Lyman (1995), will be found in a recently released draft environmental impact statement (National Park Service 1995). The complete reviews are available from the superintendent of Olympic National Park, 600 East Park Ave., Port Angeles, WA 98362.

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Literature Cited

- Dalquest, W. W. 1948. Mammals of Washington. University of Kansas, Lawrence. 444 pp.
- Fannin, J. and G. B. Grinnell. 1890. Range of the white goat. *Forest and Stream* 34:62-64.
- Houston, D. B., E. G. Schreiner, and B. B. Moorhead. 1994. Mountain goats in Olympic National Park: Biology and management of an introduced species. National Park Service Scientific Monograph NPS/NROLYM/NRSM-94/25. 295 pp.
- Lyman, R. L. 1988. Significance for wildlife management of the late Quaternary biogeography of mountain goats (*Oreamnos americanus*) in the Pacific Northwest, U.S.A. *Arctic and Alpine Research* 20:13-23.
- _____. 1994. The Olympic mountain goat controversy: a different perspective. *Conservation Biology* 8: 898-901.
- _____. 1995. Inaccurate data and the Olympic National Park mountain goat controversy. *Northwest Science* 69:234-238.
- National Park Service. 1995. Goats in Olympic National Park: A draft environmental impact statement. Olympic National Park. 270 pp.
- Schalk, R. 1993. A review of the ethnographic and archeological evidence relating to mountain goats in the Olympic Mountains. INFOTEC Research, Inc. Seattle, Washington. 59 pp. (Olympic National Park files).
- Schultz, S. 1994. Review of the historical evidence relating to mountain goats in the Olympic Mountains before 1925. pp. 256-293. *In* Houston, D. B., E. G. Schreiner, and B. B. Moorhead. Mountain goats in Olympic National Park: Biology and management of an introduced species. National Park Service Scientific Monograph NPS/NROLYM/NRSM-94/25. 295 pp.

Book Reviews

Fire Ecology of Pacific Northwest Forests

James K. Agee, 1994, Island Press. (\$50.00)

Introduction

Fires are hot topics. Both wildfires and prescribed fires capture media attention and people's imagination. Fires threaten people's lives, and tragically, people sometimes die. In the last five years, large fires in Oregon, Yellowstone, Idaho, and California have burned, drawing attention of the media, impacting local communities, and costing taxpayers millions of dollars. Fires burn places and things people value, yet fires are also critical to sustaining the ecological values of many forests in the Pacific Northwest. Fire ecology and management issues are news, often big news. Jim Agee's deft synthesis of the literature on fire ecology of forests and woodlands is a timely contribution to the public debate about fire and natural resources issues. He accurately portrays the ecological realities. Fires will occur.

"Fire is a ubiquitous disturbance . . . [that] can't be ignored" (Agee, p.3). Before Euro-American settlement, fire shaped the structure, composition, and function of most forest ecosystems in the Pacific Northwest. Fire ecology and management are central to the debates about forest and rangeland health, ecosystem management, salvage logging, water quality in streams supporting anadromous fish, and other natural resource issues in the Pacific Northwest.

Purpose

In writing *Fire Ecology of Pacific Northwest Forests*, Agee examines the effects and use of fire in forests of the Pacific Northwest. He places the ecological effects of fire in both historical and cultural perspective, and discusses many political issues in fire control and use. This timely book is rewarding for its depth, quantitative approach, and cultural perspective. Agee successfully synthesizes extensive literature into a readable, informative volume that will be of use to students, researchers, and managers. The emphasis is on

forests and woodlands of the Pacific Northwest, but the information is applicable to forests elsewhere in the western United States and Canada.

This is not a book about fire management. The author does not prescribe management direction, even for the wilderness areas, natural parks and other natural areas that have been a focus of much of his research interests. Instead he seeks to inform and improve management by increasing understanding of the ecological importance of fire in diverse forest and woodland ecosystems.

Organization

The first section of the book is devoted to discussions of the natural fire regime, and the natural and cultural environment. An overview of fire effects on vegetation and the environmental effects of fire follows the section on fire history methodology. Agee's thumbnail sketch of fire behavior, fuels, and combustion is brief but comprehensive and accurate.

In the second major section of the book, Agee explores the ecological role of fire in major forest ecosystems. In each, he includes sections on the environmental characteristics, the fire regime, stand development patterns, fuels, and management implications. The discussions are succinct.

The final chapter, "Fire in Our Future" highlights fire management in park and wilderness management, new forestry, forest health, and global climate change. Here Agee addresses the political realities and challenges of recognizing fire's ecological importance.

Strengths

Agee discusses the cultural environment of fire. This is refreshing, for all too often fire has been treated as simply a biophysical process. Agee's discussion of cultural resources and the cultural setting for fire management is deft. This provides very useful background to the final section on fire in our future, in which Agee addresses political issues, risks, and realities in fire management.

Agee draws upon the large body of literature on disturbance ecology. In doing so, he strengthens the theoretical basis of fire regime classifications.

He also addresses seasonality and extent of fires, something largely unavailable from other syntheses. The synergism with other disturbances such as insects and pathogens is discussed.

The evolutionary perspective to both cultural and ecological effects of fire is outstanding. Pacific Northwestern landscapes have changed greatly since the Pleistocene, and will continue to change in the future. The effects of global climate change on vegetation will be mediated by fire and other disturbances. Understanding past change will help managers of fires and forests in the future.

The soils and watershed section was strengthened by inclusion of a landscape approach to fire effects on whole watersheds. Hopefully, this will be the section of the book soonest to be out-of-date, as the short review reflects our weakness in this area.

The text is well organized. I located both major and minor topics through the index. The literature for all chapters is cited in a single section, making it easy to identify likely sources for additional reading.

Weaknesses

The fire history section had one serious weakness. Given the current focus on landscape-level issues, I sought a discussion of systematic sampling for an entire landscape. Unfortunately, most of our data on fire history are data from points where fire scars and age structures are easily interpreted, typically southwestern-facing slopes where fires readily scar trees. For managers seeking answers to quantify the historical or natural range of variability over entire watersheds, this is a major

shortcoming. Furthermore, a discussion of the concept of historical or natural range of variability would have been a natural extension of the evolutionary perspective of the book. Given the extent to which historical range of variability is appropriately and inappropriately used in management decisions, I found this to be a great weakness.

Few nonforested ecosystems are discussed. The exceptions are a few pages on subalpine communities. Riparian systems are largely excluded, although Agee discusses both landscape and finer scale effects of fire on soil and water. Oak and western juniper woodlands are also discussed. However, no other nonforest types, such as sagebrush, Rocky Mountain juniper, or grasslands are covered. Yet these types are widely distributed in the Pacific Northwest, and are the focus of great debate about natural resource management. Such material was beyond the stated scope of the book, but should have been included.

Summary appraisal

Fire Ecology of Pacific Northwest Forests is a useful reference and text for students of fire ecology and management. Natural resource managers will also find this a handy guide to the complex field of fire ecology. All of us, who study and work with fire, will benefit from the evolutionary and cultural perspectives presented by Jim Agee.

— Penelope Morgan
Department of Forest Resources
University of Idaho
Moscow, Idaho 83844-1133

Wildlife Ecology and Management

Graeme Caughley and Anthony R. E. Sinclair,
1994, Blackwell Scientific Publications. (\$45.00)

The scope of Caughley and Sinclair's *Wildlife Ecology and Management* is well defined and focused. They strictly define wildlife management as the management of wildlife populations. In this context, the wildlife manager has four distinct options when managing wildlife: 1) make the populations increase, 2) make the populations decrease, 3) harvest a sustained yield from the population, or 4) take no action except to monitor the population. In this book the authors' goals are: to provide future managers the necessary ecological background to understand the ramifications of these management options, and to examine practical aspects of achieving these options such as animal censusing, managing endangered species, wildlife harvesting, and control of wildlife pest species.

In the Introduction, the authors define wildlife and wildlife management and describe how wildlife management should operate. The authors restrict their definition of wildlife to free-ranging birds and mammals, although they do acknowledge that the term can have a broader definition. The description of how wildlife management operates examines the process of decision analysis. The authors make an important distinction between value and technical judgments and stress that value judgments are inherently subjective whereas technical judgments must be objective and based on realistic objectives.

Chapter 2 introduces a section on the ecological underpinnings of wildlife management by providing an overview of the natural history of the world's biomes and reflects the extensive field experience of the authors in many of these biomes. In the following nine chapters, Caughley and Sinclair address the principles of wildlife ecology by examining a range of topics including adaptations of individual animals, dynamics of wildlife populations, patterns of distribution of wildlife species, interactions of wildlife species with their food resources, intra- and interspecific competition, parasites, and diseases. Given the breadth of the material that the authors cover in a relatively brief format, it is not surprising that these chapters vary from somewhat superficial to ex-

cellent. For example, the chapter entitled "Animals as individuals" introduces the student to 1) how evolutionary processes such as speciation, convergence, and radiation shape individual adaptations, 2) how these adaptations are limited by phylogenetic and geographic constraints, 3) how genetic variability within and between populations can be measured by allozyme electrophoresis, restriction fragment length polymorphisms, DNA fingerprinting, mitochondrial DNA, or polymerase chain reaction, and 4) why this information is useful for wildlife managers. All this is covered in about 14 pages of text. Although it is very positive that this information is included in an undergraduate wildlife management text, a student without a strong background might feel a bit overwhelmed. Although the authors help students through the material by providing relevant examples with citations to illustrate most topics, some topics in this chapter are not supported with this information. The chapters on "Dispersal, dispersion and distribution" and "Parasites and pathogens" similarly attempt to cover broad topics in a condensed and somewhat superficial format. In contrast, most of the other chapters in this section provide students with a solid foundation of both theoretical and practical knowledge. For example, the chapter on "Animals in populations" guides students through an introduction to the theoretical aspects of population dynamics and the relationship between populations and their resources to the practical aspects of the construction of life tables and use of logistic equations. The chapters on "Resources and herbivory" and "Food and feeding" provide students with an understanding of the interactions of herbivores and their food resources and methods to assess food availability and animal requirements.

The final section in the text covers practical applications of wildlife ecology in six chapters on counting animals, experimental management, conservation, and wildlife harvesting. Given their background, it is not surprising that the authors' discussion of counting animals is comprehensive and filled with their insights into the applicability of different census methods under varying circumstances. The authors introduce their chapter on experimental management by differentiating between "traditional" and "experimental" modes of wildlife management. They suggest that judging the usefulness of new management ideas is best accomplished by an experimental approach

and provide an excellent overview of the basic principles of experimental design using examples that wildlife students should find relevant. The next two chapters address theoretical and practical aspects of wildlife conservation. Chapter 14 examines how environmental, demographic, and genetic factors might contribute to the extinction of a species. The authors stress that the commonest causes of extinctions are caused by humans modifying the habitat or introducing new elements (e.g., predators, competitors, pathogens) into the environment. Chapter 15 reviews 12 case studies of species driven to or near extinction by a variety of human actions. Building on these case studies, the authors then examine approaches to the diagnosis of causes contributing to the decline of a species and to the rescue and recovery of near extinct populations including conservation in parks and reserves and international conservation. The next chapter on wildlife harvesting examines the types of information a manager must have to develop harvest strategies that result in a sustainable yield without jeopardizing populations, the trade-offs between differing harvest approaches, and the differences between recreational versus commercial harvest. The objectives of any wildlife control program, the topic of the book's final chapter, must be defined precisely by the desired benefits of the program, not simply by numbers of animals to be removed. The authors outline different control methods (mortality control, fecundity control, and indirect methods such as habitat manipulation) and discuss the decision process to determine the appropriateness of control methods.

The chapters in this text are well organized and allow the reader to follow the sequence and development of topics. Each chapter is prefaced by a concise introduction that provides both an outline of the information to be covered in the chapter as well as a conceptual framework for that information. Summaries at the end of each chapter recap major points. Section headings offset in the left margin facilitate the organization of material. Given the breadth of material covered in many chapters, suggested readings at the end of each chapter would be helpful for students needing more background information on a subject. The authors support their topics with ample ref-

erences that represent a good mixture of benchmark studies and current research. A cross reference to the section in the book where an article is cited or an author index would provide additional supporting information for students. In contrast, the Appendix that provides two tables listing critical values for F and for Cochran's test are unnecessary.

In summary, the defined focus of Caughley and Sinclair's *Wildlife Ecology and Management* represents both its weakness and its strength. The restricted, focused definition of wildlife, as primarily free-ranging birds and mammals, is unfortunate. The text covers many current aspects of wildlife management and should recognize that increasingly wildlife managers are tackling problems of managing populations other than free-ranging birds and mammals. By focusing on the strict definition of wildlife management as the management of wildlife populations, I fear the authors might have reduced the usefulness of the text in management classes. Introductory courses at institutions with broad wildlife and natural resource management programs often include more general topics of wildlife management (e.g., history of wildlife, management systems, habitat management). Advanced courses at such institutions typically require that students already have courses in animal ecology and population dynamics. In contrast, institutions with less comprehensive programs often need to cover a breadth of topics in a single course. Nonetheless, by focusing on the management of wildlife populations, the authors have integrated a great deal of information on population management and have ensured that the integrated topics are of current concern. The text will definitely be useful for instructors developing courses. Instructors might decide to adopt this text and supplement other topics with outside readings. Additional readings should include original research articles by the authors. The text brings together the collective experience of two renowned wildlife biologists, and an appreciation of their research activities enhances the reading of their text.

— Margaret A. O'Connell
Biology Department, MS 72
Eastern Washington University
Cheney, WA 99004

The Landscapes of Craters of the Moon National Monument: An Evaluation of Environmental Changes.

R. Gerald Wright and Stephen C. Bunting, 1994, University of Idaho Press. (\$24.95)

The words "Craters of the Moon" may bring to mind a dry, barren landscape devoid of plant and animal life. While this area of the Snake River Plain in southern Idaho is a harsh environment, it is far from lifeless. Major plant communities include aspen, Douglas-fir, and limber pine forests, sagebrush/steppe communities, and a variety of species that colonize the lava fields.

The harsh environment and lava fields discouraged settlement and livestock grazing. There was little human use of natural resources prior to establishment of the 54,000-acre Craters of the Moon National Monument in 1924. Since then, areas within the Monument have been protected. Further protection was added in 1970 when 80 percent of the Monument was designated as wilderness. Much of the Monument is in pristine condition, which is unique by itself. Adding to the uniqueness is the fact that most plant communities are examples of primary succession, including succession on lava flows and plant communities typical of those indigenous to the Snake River Plain.

Relatively few studies investigate environmental changes over several decades. Matched photographs show changes that occur over decades, and the same photographs are available to future generations. The existence of historical photographs made it possible to conduct a study of vegetation changes in the Monument. Wright and Bunting match 34 contemporary photographs with photographs taken from 1923 to 1965 to illustrate changes over time. The result of their work is a book that is a delight to study.

Introductory material includes short sections on history and exploration, geology, soils, climate, vegetation, visitor use, concepts of environmental change, and the use of matched photos to evaluate environmental change. This is all excellent background information for the main part of the book—the 34 matched pairs of photographs.

Wright and Bunting did an exceptional job of finding photo points for the historical photographs.

This is impressive because photo points were not established by the original photographers. In fact, the historical photographs were not taken for purposes of studying environmental changes. Their purpose was to document exploration of the area, to plan for development of the Monument, and as scenic photographs.

Matched pairs of photographs illustrate changes in limber pine density, changes in Douglas-fir density, changes in aspen communities, the effects of fire, the constancy of plant distribution patterns in shrub communities, the stability of lava flows, and changes associated with Monument development. Important relationships and changes observed in the photographs are discussed. Following the photographs is a discussion that summarizes and interprets information from the study.

This book will be of interest to a broad spectrum of readers, from those with a general interest to those interested in scientific inquiry. Discussions are thorough but not too long or technical, and the photographs are interesting from many perspectives—history, geology, ecology, wilderness, etc.

Unfortunately, the book also contains errors. They should be easy to correct. Plate 11A (historical photograph) is thought to have been taken in 1932, but the buildings under construction are too modern for 1930s architecture. The photograph year on plate 29A is 1957, but the photograph clearly shows cars from the late 1920s to early 1930s. Plate 30A is thought to have been taken in 1930, but vehicles in this picture are from the early to mid-1950s.

Other concerns include contradictory information on whether the highest elevation in the Monument is 7,160 or 7,696 feet, possible misidentification of photo points on maps, Figure 1 does not show the northwest portion of the wilderness boundary, and a photographer's shadow is discussed in the caption for plate 22A, but there is no shadow.

The book is a historical reference of the Craters of the Moon National Monument. With its publication, the authors' contemporary photographs become historical photographs. Current and future readers will rely on the accuracy of information presented. At a minimum, readers will want an erratum included with their purchase of the book.

Wright and Bunting's work will motivate others to conduct similar studies. The value of permanent plots is illustrated, which should generate interest in conducting long-term studies. Hopefully, this study will raise the public's awareness of the dynamic nature of plant communities. Information gathered from such studies will add to our understanding of ecological processes

and assist managers in making sound decisions about natural resources.

—Dennis E. Ferguson
USDA Forest Service
Intermountain Research Station
1221 S. Main
Moscow, Idaho 83843

Plants of the Pacific Northwest Coast

J. Pojar and A. MacKinnon, editors, 1994, British Columbia Ministry of Forests and Lone Pine Publishing.

Plants of the Pacific Northwest Coast is a full color field guide to the vegetation of the northern Pacific coastal region, a 1,600-kilometer narrow band from the southern Oregon Cascades to Alaska's Prince William Sound. The main body of the text contains over 1100 color photographs, 1000 line drawings, and 794 range maps with descriptions of common vascular plants, bryophytes, and lichens native or naturalized to the region. The species entries are organized and color coded by family or functional group (trees, shrubs, wildflowers (by family), aquatic plants, oddballs, grasses, sedges and rushes, ferns, clubmosses and horsetails, mosses, liverworts, and lichens). An introductory section provides an integrated description of the diverse climates, physiography, geology and vegetative communities of the region, as well as uses of plants by people.

Plants of the Pacific Northwest Coast should appeal to a wide audience. The information is clearly organized, artistically presented, and easily used by the beginner and experienced botanist alike. The combination of photographs, line drawings, comparative charts, and dichotomous keys for difficult genera provide key information that allows readers to rapidly identify plants and cryptogams. The line drawings comparing leaf shapes or handlens characters within families and genera are particularly handy. Although we would have liked to see family names included for the page headers of "Other Families, Aquatics, Oddballs," these names are provided on the first page of this section.

The Ecology and Notes sections for each species are particularly impressive. They feature interesting facts about Native American uses of plants, taxonomy, derivation of scientific names, and natural history which should be very useful to interpretive specialists throughout the Pacific Northwest. The combination of plant identification with ecological and ethnobotanical information sets this book apart from other popular and scientific plant guides for this region.

As Forest Service professionals routinely engaged in identification and inventory of vegeta-

tion, we were curious about how comprehensively the guide would cover specific national forests. We calculated species coverage of vascular plants for our own Siuslaw National Forest, along the central Oregon coast, and found that the guide encompassed approximately 83% of the vascular plants (it covered 55% extensively with photos and plant descriptions; and referenced the other 28% in the Notes section with information to help differentiate similar species). All commonly occurring species were included. The missing elements were primarily rare species (e.g. some of our state-listed threatened and endangered species), aquatic species, and a few common exotics (e.g. certain species of *Trifolium*). The percentage of species covered dropped a little going north. For example, the guide covered about 65% of the 1000 known vascular plants in the Tongass National Forest, which encompasses most of Southeast Alaska. Of those, 36% were fully-featured with color photos.

We did notice that as a guide to total vegetation, the larger the organism, the more likely it was to be included. The guide covers virtually all native tree species from the region, at least half of the remaining vascular plants, but less than 15% of known mosses and lichens. An ecological or biodiversity emphasis would have better equalized the proportion of species represented. However, we realize that this would have significantly increased the size of the guide, which already verges on being too big to fit in one's pocket.

Lichens are particularly diverse and conspicuous in the Pacific Northwest where they play significant ecological roles and contribute to the vegetative biodiversity and uniqueness of the region. It is therefore appropriate and pleasing to see them included in this manual. This is the first major guide in North America to introduce common names for lichens—a step which should improve their accessibility. We found this section offers a solid, helpful introduction to common, easy-to-recognize lichens with good color pictures, drawings and entertaining descriptions and facts regarding lichen ecology, ethnobotany and origin of Latin names. The only drawback is that it leaves us wishing for more! Although one could walk in any natural area of the Pacific Northwest and find species covered in this book, it would be frustrating to use for inventory purposes or other situations where a large percentage of species need to be identified.

Plants of the Pacific Northwest is a valuable field guide for our area. We strongly recommend this book for amateur naturalists and resource specialists alike, especially for those interested in the vascular plants of the Washington and Oregon coast and an accessible introduction to lichens and bryophytes.

—Linda Geiser and Katie Grenier
USDA Forest Service
Siuslaw National Forest
P.O. Box 1148
Corvallis, Oregon 97339

Shorebirds of the Pacific Northwest

Dennis Paulson, with illustrations by Jim Erckmann, 1993, University of Washington Press. (\$40.00)

Shorebirds make up a large part of the Pacific Northwest's avifauna. Spring and Fall migrations bring millions of these birds along our coasts and through our interior. Many species find breeding habitats here, and millions will winter here as well. Most recent monographs on shorebirds have focused mainly on identification, and have generally been undertaken at a national or global scale. However, few books attempt to document patterns of occurrence or examine fine differences in plumages at a local scale. Considering the importance of the Pacific Northwest to shorebirds, and the continual loss or degradation of habitat for these species, it is good to see a monograph which helps to further our understanding of shorebirds in our region.

Shorebirds of the Pacific Northwest, written by Dennis Paulson, is an attempt to fill in the gap left after using field guides, books which generally are limited to help with species identification. Dennis has packed this book with facts regarding temporal and spatial patterns of shorebird distribution in the region, plus tips for identification of similar species in multiple plumages. It is organized in 5 basic parts: overview, introduction to shorebirds, temporal and spatial shorebird patterns, a systematic approach to shorebird identification, and species accounts. The last section accounts for 70% of the book's volume.

The first section is an overview, discussing scope and purpose. A map shows the book's geographic limits of Idaho, Oregon, Washington, western Montana (west of the Continental Divide), and southern British Columbia (south of latitude 51 N). Paulson goes on to subdivide the region along the Cascade Crest, a useful distinction when discussing shorebird distribution in this region. Several distinct ecoregions are also named, and their locations described. The species discussed in the later text are outlined briefly in this section, along with the author's defense of which species to include or exclude, and 2 tables giving recorded dates for species along with their latin names. Paulson has made an attempt to keep this book current beyond its publishing date by also including a few species he anticipates will occur in the region in the near future. Another use-

ful feature is a discussion of useful references for shorebirds.

The second section is an overview of shorebird anatomy, plumage, flight patterns, and vocalizations, with an emphasis on using this knowledge to aid in identification. The author has made a tremendously useful resource in this section, by explicitly outlining the physical characteristics used to distinguish shorebirds, and by utilizing detailed drawings showing these distinctions. A series of tables provides a key to aid identification as well. One real benefit of using this book is the continued reference in the species accounts to the terms described in this section. Paulson first defines many terms for plumage and shape, and then uses them consistently later in the species accounts. If any terms used later in the species accounts became confusing, the remedy was to refer back to this section.

The third section is justly titled *Shorebirds in Time and Space*. It follows Pacific Northwest shorebird movements throughout the year, and discusses activities occurring during the year. Several tables show the geographic origin (Eurasian/American) of species, and their seasonal abundance. Species are also treated by groups based on breeding areas and migration routes, discussing commonalities and differences between and within groups. Finally, a discussion of shorebird concentration is given, focusing on Northwest species and their habitat needs, as well as giving useful information about how the amateur naturalist can contribute with data.

Shorebird identification is the fourth section, which outlines methods to employ when trying to distinguish between species. The first part discusses systematic approaches involving fieldmarks and identifying unique groups of birds, and outlines specific problems encountered with shorebirds. It goes on to include a qualitative table for bird groups, showing which species share characteristics and which ones do not, and includes all plumages. This borders on being a key, but lacks the decisions of a true key to species. This part of the book is useful, but would be an even greater tool if it was organized into a dichotomous key.

The final section, which constitutes the large majority of the book, is a species by species account of all shorebirds occurring in the Pacific Northwest, plus a few that are expected to be found

in the near future. Each account outlines the species status and distribution within the Pacific Northwest, giving dates for arrival, peak number, and departures, as well as discussing the origin and destination of each species' migratory trip. A highly useful bar chart shows graphically the temporal distribution on each side of the Cascade Crest. Maps are included for breeding species. Plumage characters are also discussed in great detail, using the terminology defined in earlier sections to avoid confusion, and supplemented with color photographs. Unlike some picture-based field guides, these photos are high quality, taken in good light, and are identified correctly. They are a tremendous asset when trying to distinguish between similar-appearing species. The photos are limited to species which have ID problems associated with them, to avoid cluttering the book. Many species also have tables showing diagnostic characters for different plumages. Each species (except Sanderling—an editorial error) also has notes on vocalizations which are useful, as far as any text description of an avian voice can be. Other features of this section include notes and questions regarding each species, plus references to published photos and records. The author has also recorded references where photos have been misidentified, supplying the correct species name.

One failing of this book is its inadequate use of maps. For example, in the overview, a map is

used to describe the geographic limits of the book, but not to show the coast or interior regions, or any of the smaller ecoregions within. This will undoubtedly cause confusion among readers unfamiliar with the area. Another useful resource (not included) would be species geographic distribution maps in various seasons, which would be far easier to comprehend than reading several paragraphs of written information. Instead, only breeding maps are given.

Dennis Paulson has met his goal in writing this book. Early on he states "this book is intended to be a supplement to field guides...", which is a very good description of *Shorebirds of the Pacific Northwest*. It easily takes up where the field guides leave off, providing the reader with facts about every aspect of shorebirds in the region, and providing the tools to go beyond the identification skill levels found in field guides. The amount of information and the organized presentation provide a book that will be a standard reference for years to come, while remaining concise enough to be taken in the field.

—Michael R. Smith
Washington Cooperative Fish and
Wildlife Research Unit
University of Washington, WH-10
Seattle, WA 98195

More Tree Talk: The People, Politics, and Economics of Timber

Ray Raphael, 1994, Island Press (\$17.00 paper, \$40.00 hardbound)

In this era of timber wars in the West, one cannot pick up a book about forests without wondering which side it will take. *More Tree Talk: The People, Politics and Economics of Timber* begins with the declaration that "The old-growth forests are almost gone," leading the reader to expect a preservationist's lament. However, the second sentence reads "Loggers are out of work," conjuring yellow ribbons of the Save-our-Sawmills brigade. Recognizing that "each side vilifies its opponents," author Ray Raphael walks a careful line between the two in his description of the politics, economics and ecology of forest management.

More Tree Talk updates *Tree Talk*, which some say put Island Press on the map. As in the first, the heart of this book is local voices of people working and living in the region. Raphael frames his interviews with his own well-written arguments, supported by scientific research and public documents. This combination is enriched by pen-and-ink drawings of, e.g., test-tube timber, a scarification plow, and mycorrhizal fungi.

The first chapter puts the contemporary forest crisis in historical perspective. Raphael quotes Gifford Pinchot, creator and first Chief of the Forest Service: "The United States has already crossed the verge of a timber famine so severe that the blighting effects will be felt in every household in the land" (p. 13). President Bill Clinton's 1993 Forest Conference was anticipated by Teddy Roosevelt's 1908 White House gathering of governors, members of the Cabinet and Supreme Court, scientists and conservationists who adopted a "Declaration of Principles" which acknowledged not only the diminishing timber supply and the importance of forests for protection of streams, but the responsibility of private forest owners to protect their lands.

"Voice of Industry," Chapter 2, provides insight into the industry perspective (and a hint of bias from the author). Raphael writes that in industry's perspective virgin forests were "wasteful: the rate of decay in 'overmature' timber often equaled or surpassed the rate of growth, bringing

net productivity to a standstill.... The old growth was liquidated to make room for young, fast-growing trees" (p. 27). Gifford Pinchot, whom Raphael pointedly labels here as "the famous conservationist in the early 1900's" (p. 28), is then presented as an early promoter of the agricultural model "Forestry is Tree Farming."

In one interview, an officer of the Industrial Forestry Association persuasively details the economic risks and challenges of achieving success as a lumberman (fire, insects, property taxes, government regulation and long-term investment). Raphael's editorializing can be seen in another selection of the man's words, "Forestry has always been an environmental undertaking. Its main thrust has always been taming the wild forest for man's use and enjoyment by managing the ecology, instead of letting it run rampant as though there were no people around" (p. 33). Raphael likens the even-age monoculture of tree farms to the corn-fields of standard farming practices. After quoting the manager of forestry research for Georgia-Pacific Corporation on the science of reforestation (including genetics, "release spraying," aerial fertilization and precommercial thinning), Raphael observes that, "For every crisis that planted trees may encounter, there is a chemical substance to aid and comfort them" (p. 43).

The last chapter of this background is titled, "Tree Saving, the Voice of Ecology." Gordon Robinson, a forester for the Sierra Club, is the subject of the first interview, but the chapter's emphasis is on ecology, not the environmental movement (neither national nor local efforts by environmental organizations are analyzed in this book). Interviews and scientific research demonstrate the importance of diversity in forest ecologies and the shortsightedness of managing for a single product. Monocultures lead to increased ecological vulnerability; pesticides destroy small animals who aid in genetic diversity and mycorrhizal fungi distribution. Interviews with a hunter/lumberjack and a director of a fishermen's association demonstrate the threats of current logging practices to soil and stream health, and the importance of replacing intensive management with "ecosystem management" which protects biological diversity and recognizes that "all elements are linked, that the whole is created by the interrelationship among the parts" (p. 79).

Part II, "Working it out on the Ground," presents new forestry strategies addressing issues

raised in Part I. Chapter 4 describes holistic forestry, which seeks to minimize its intrusion on ecological systems by developing harvesting strategies that "simulate nature's own management schemes" (p. 84). Raphael presents experiments, on the ground and in laboratories, in sustainability of forest ecosystems and their broad range of associated economic values.

The last chapter in Part II discusses harvest technology: new machines such as catskinners which lessen the damage to forest floors (but may not live up to their promises); old-fashioned horse logging (which is easier on the soil, but limited to small timber); cable yarding, balloon and helicopter yarding (gentler, but still with limitations and high costs).

Part III moves to political economic questions, topics seldom integrated with those introduced earlier (even the first *Tree Talk*). Chapter 7 discusses corporate profit issues related to timber companies and decision-making criteria in managing industrial and public lands. Reinvestment and externalities do not figure as largely as capital opportunity costs and discount rates. Accordingly, the "economic maturity of timber occurs long before the productive maturity" (p. 163). Economic maturity determines when trees are harvested, although harvesting at productive maturity "could have obtained two and a half times the quality sawtimber in a shorter period of time" (p. 166). The structure of capital drives decision-making, "but it is based on a logic that has nothing at all to do with silviculture or ecosystem management" (p. 169). Nontimber values such as water quality, fisheries and wildlife habitat do not figure in, nor do costs of pollution. This chapter ends with examples of companies and other possible ownership arrangements which might manage for long-term forest health and profit.

Chapter 8 describes the significance of public lands for Western rural communities and timber supply, and the remoteness and politics of resource management decisions. As in the chapter on economics, Raphael points out the contradiction between functional (bureaucratic rules, regulations, targets, and funding mechanisms) and substantive (scientific, on-the-ground decisions, ecosystem health) decision-making. Raphael's primer on forest policy (explaining MUSY, NFMA, ASQ, K-V, etc.) is useful and accurate, although

it draws largely on authors and publications known for their criticism of the Forest Service (e.g., Randal O'Toole and *Inner Voice*), and the interview he shares is with a member of AFSEE (Association of Forest Service Employees for Environmental Ethics). The chapter ends with an informative explanation of Clinton's Forest plan, questioning the possibility of bureaucratic transformation necessary for the new vision of ecosystem and adaptive management.

Non-industrial private forests (NIPF's), although representing only a small percentage of forest lands, hold a significant source of timber; Chapter 9 discusses (somewhat romantically) the potential for sustainable management on these lands. While Raphael is critical in his discussion of the politics of regulating these lands, he fails to discuss the current economic incentive and pressure from a log-hungry industry to liquidate these private forests.

The final part of the book ties the ecological, economic and political issues to the lives of people in timber communities. Interviews describe communities losing their youth, torn apart by battles between local environmentalists and timber workers, and brought together by coalitions to save both communities and forests, which depend on one another. Raphael and his interviewers suggest ways to reinvest in sustainable forests and rural community development.

Given the current politics of federal forest management in the United States (Congress pressing once again to get out the cut, rural westerners mobilizing to turn federal lands over to the states, and challenges from all sides to the President's Forest Plan), citizens need access to comprehensive, yet accessible, discussions of all sides of the issue. This book will engage the general reader. No doubt timber industry and federal agency workers will find Raphael's critiques one-sided and foresters and ecologists may find his writing naive; nonetheless, the range and passion of the voices of the thirty-one interviewees and the breadth of the analysis counterbalance any superficiality.

—Victoria Sturtevant
Department of Sociology and
Anthropology
Southern Oregon State College
Ashland, Oregon 97520

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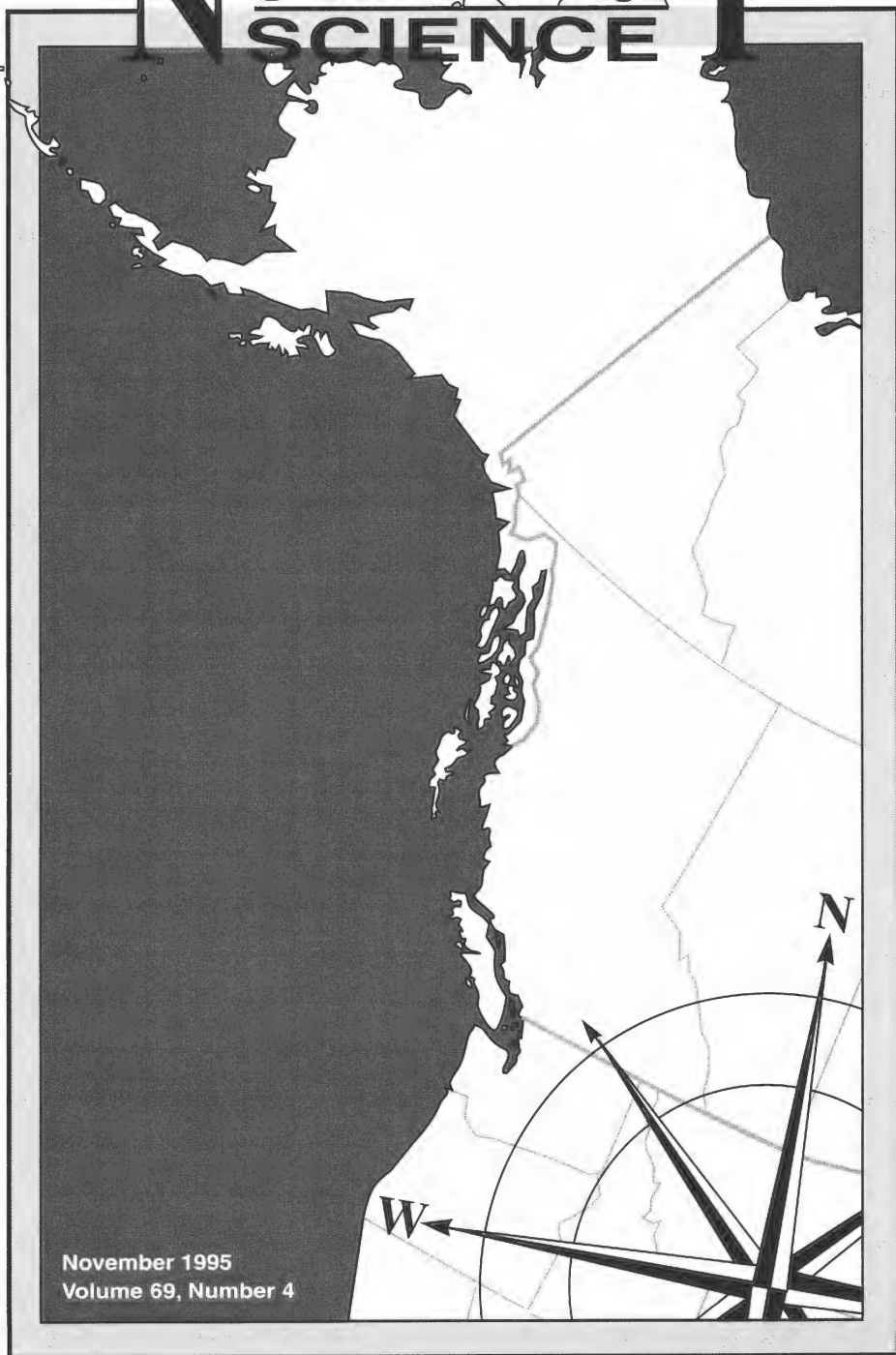
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Editor of *Northwest Science*

David L. Peterson
Cooperative Park Studies Unit
University of Washington, Box 352100
Seattle, Washington 98195
Telephone: 206-543-1587, Fax: 206-685-0790
Internet: wild@u.washington.edu

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Pacific Lutheran University
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Telephone: 206-535-7565
Fax: 206-536-5055
Internet: hansendh@plu.edu

*Term of office expires in the year given in parentheses.

Book Review Editor

Jerry O. Wolff
U.S. Environmental Protection Agency
200 SW 35th Street
Corvallis, Oregon 97333
Telephone: 503-754-4377, Fax: 503-754-4338
Internet: jerryw@mail.cor.epa.gov

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Announcements

Notice of Annual Meeting

The 69th annual meeting of the Northwest Scientific Association will be held jointly with the Wildlife Society and Lichen Guild on 20-23 March 1996, at Pacific Lutheran University in Tacoma, Washington. In addition to several contributed paper sessions, there will be symposia on climate change in the Pacific Northwest, geology of the Olympic Peninsula, and the Eastside Forest Assessment. There will be field trips focusing on various aspects of natural resources of the Olympic Peninsula, Nisqually Wildlife Refuge, and Puget Sound region. Both members and non-members of the Northwest Scientific Association are welcome at the meeting, and students are especially encouraged to attend.

A more detailed meeting announcement and registration information will be mailed to NSA members in the near future. For information about presenting papers, contact: Dr. Jan Henderson, 206-744-3462.

1996 Student Research Grant

Student Research Grants are provided by the Northwest Scientific Association to help students complete scientific research projects. Funding should be used only to support research activities of the student. It is expected that students will report their research results at a future NSA meeting.

Eligibility — Applicants must be regular members of the Northwest Scientific Association. *Northwest Science* contains information for joining the society.

Preparation of the Proposal — A cover page should include: (1) name and address of applicant, (2) associated institution, (3) name of major professor/advisor, (4) degree program, (5) year in school, (6) amount of funding requested (maximum of \$500 [US]).

The proposal should include: (1) title, (2) statement of justification, (3) methodology/study design (including analytical methods), (4) detailed budget. The proposal should be no more than three typed, double-spaced pages (excluding cover page and budget).

Proposals are due on or before 7 February 1996, and should be sent to: Dr. Jerry O. Wolff, U.S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, Oregon 97333 (tel.: 503-754-4377, fax: 503-754-4338, email: jerryw@mail.cor.epa.gov). Grants will be awarded at the 1996 annual meeting of NSA.

Associate Editor Changes

Dr. Gary L. Sheldon, Associate Editor for Engineering and Mathematics, is stepping down from his duties with *Northwest Science* after 7 years of service to the journal. He is retiring this year from the faculty of Washington State University (Vancouver). We are grateful for Gary's contributions as Associate Editor, and wish him all the best in the years ahead.

Because of increased interest in book reviews in *Northwest Science*, the new position of Book Review Editor has been created. Dr. Jerry O. Wolff, a wildlife biologist with the U.S. Environmental Protection Agency in Corvallis, Oregon, has agreed to serve as Book Review Editor for the journal. We appreciate Jerry's willingness to take on this responsibility. If you know of a book that would be of interest to our readers, please contact him with the appropriate information (see the journal inside cover for his address).

...And One More Change

You may have noticed that *Northwest Science* is now being published in Times font. Hopefully you will find that this change improves the visual appearance of articles published in the journal.

Gradient Analysis of the Vegetation in a Lagoonal Salt Marsh, Whidbey Island, Washington

Abstract

Lake Hancock on Whidbey Island, Washington, supports a 69 ha euhaline lagoonal marsh. North of California, marshes of this type are rare and usually less than 30 ha. Brackish deltaic marshes comprise most of the coastal wetlands from Oregon to southeast Alaska. The Lake Hancock environment is unique among the marshes of the Pacific coast; consequently the marsh vegetation also is unique. The Lake Hancock marsh supported a single community dominated by *Salicornia virginica*. *Triglochin maritimum*, *Distichlis spicata*, and *Jaumea carnosa* were minor marsh components. Elevation and soil moisture most influenced the vegetation. Both the environment and vegetation of the Lake Hancock marsh are more similar to the marshes of central and southern California than to the marshes of Oregon, Washington, British Columbia, and Alaska.

Introduction

Coastal marshes border the ocean where they are flooded periodically by sea water, making them transitional between terrestrial and marine systems. Although they comprise features from both of these environments, they have characteristics more typical of wetlands. Coastal marshes occur in shallow bays protected by baymouth bars, or in areas supplied with river or marine sediment but protected from high energy waves by spits or barrier islands (Chapman 1976). The slope of the surrounding upland determines the marsh size. Steep slopes, such as those of the fjords of Norway, produce narrow marshes while gentle slopes lead to wide marshes (Chapman 1976). The major physical features of coastal marshes are salt pans, unvegetated areas often filled with water, and a system of channels that carry water throughout the marsh (Chapman 1960). In general, coastal marshes are best developed at mid- and high latitudes.

There are three types of coastal marshes (Newby 1982). Lagoonal marshes, the subject of this paper, form on marine sediments where a bar has grown across an irregular coastline, or on river sediments where spits have partially blocked a river mouth. Deltaic marshes form in river deltas, and fringing marshes develop in estuarine systems, such as Chesapeake Bay. Compared to deltaic and fringing marshes, lagoonal marshes have better shelter from tide and current action, soft mud or sand substrates, a well-mixed water column, and stable gradients that do not fluctuate with the tides (Barnes 1980).

Often the same genera and sometimes the same species are found in salt marshes of widely separated geographic regions, and the vegetation usually is grouped into distinct zones that correspond to changes in environmental factors (Adams 1963). Those factors most responsible for the vegetation zones are elevation, inundation, salinity, aeration, soil water, soil texture, and water table depth (Purer 1942, Hinde 1954, Chapman 1960, Adams 1963, Ranwell 1972, Eilers 1975, Jefferson 1975, Disraeli and Fonda 1979, Burge et al. 1980, Ewing 1983, Dawe and White 1986, Snow and Vince 1984, Callaway et al. 1990).

Much of the data on North American coastal marshes has come from work done in Atlantic coastal marshes, particularly those of the coastal plain. The vegetation, successional patterns, and energetics of these marshes have been carefully studied (Ganong 1903, Conard 1924, Chapman 1940, Miller and Egler 1950, Penfound 1952, Teal 1961 and 1962, Adams 1963, Redfield 1965 and 1972, Blum 1968, Udell et al. 1969, Nixon and Oviatt 1973, Bertness and Ellison 1987, Hartman 1988, and many others). From 80% to 90% of the Atlantic coastal plain is suitable for marsh development (Glooschenko 1980); currently marshes cover nearly 600,000 ha of the Atlantic coast (Reimold 1977). *Spartina alterniflora*, the most ubiquitous species, ranges from Newfoundland to southern Florida (Reimold 1977).

In contrast, the marshes of the North American Pacific coast have received less attention (Chapman 1960, Vince and Snow 1984). The geomorphology of the Pacific coast is not

conductive to extensive marsh formation (Chapman 1960, Eilers 1975, Bradfield and Porter 1982, Vince and Snow 1984); only 10% to 20% of the coastline comprises potential marsh sites (Glooschenko 1980). The marshes of southern California exist around lagoons, while marshes of more northern latitudes have developed almost entirely in deltic and estuarine areas (Eilers 1975, Glooschenko 1980, Hutchinson 1982, Callaway et al. 1990). These developmental differences create important phytogeographic differences along the Pacific coast, as compared to greater similarities among marshes on the Atlantic coast.

The lagoonal marshes of southern California have been studied comprehensively by Purer (1942) and Vogl (1966). In her study of the marshes of San Diego County, Purer (1942) recorded euhaline to hyperhaline conditions throughout the growing season, and subdivided the littoral zone into three vegetation zones. While she provided no quantitative vegetational data on these zones, she did state that the lower zone was dominated by *Spartina foliosa*, the middle by *Salicornia virginica* and the upper by *Monanthocloe littoralis*, *Atriplex watsonii*, and *Frankenia grandifolia*. Vogl (1966) also reported three zones in his study of the Upper Newport Bay marsh, near Los Angeles. He provided cover data for the species in each zone (Table 1) and stated that this marsh was similar to those studied by Purer (1942). Vogl (1966) noted that *Salicornia virginica* was the most important species in the Newport marsh.

TABLE 1. Mean percent cover for common marsh species in the three zones of the Upper Newport Bay, California, marsh (compiled from Vogl 1966).

Species	Lower	Middle	Upper
<i>Spartina foliosa</i>	38	1	-
<i>Salicornia virginica</i>	4	23	40
<i>Batis maritima</i>	4	15	1
<i>Triglochin maritimum</i>	-	11	1
<i>Distichlis spicata</i>	-	2	5
<i>Monanthocloe littoralis</i>	-	-	15
<i>Scirpus californicus</i>	-	-	14

Callaway et al. (1990) studied a fringing (estuarine) marsh at Carpinteria, California. Although their study focused exclusively on marsh vegetation that began 85 cm above mean sea level, they

described three vegetated zones, the lowest of which was dominated by *Salicornia virginica*. This low marsh zone at Carpinteria appears to correspond to the upper marsh zone of Newport Bay (Vogl 1966), insofar as they both were dominated by *Salicornia virginica*. Otherwise, only *Distichlis spicata*, and *Monanthocloe littoralis* were common to both marshes.

Several important California marsh species, most notably *Spartina foliosa* reach their northern limits in California. North of California the large amounts of fresh water input into the deltic marshes dilute the salinity to brackish conditions. In response to this salinity change, true salt marsh species, such as *Salicornia virginica*, *Distichlis spicata*, and *Triglochin maritimum* (Glooschenko 1980) are replaced by brackish species like *Carex lyngbyei* and *Scirpus americanus*. *Salicornia virginica* is present in some marshes primarily as a mudflat colonist, but its overall community role is much reduced.

Macdonald (1977) classified the Pacific coast marshes according to vegetation and location (Table 2). His groups accurately described most of the marshes of the Pacific Northwest. Macdonald chose *Carex lyngbyei* as the indicator species for Oregon, Washington, and British Columbia, a choice strengthened by recent studies in those regions (Disraeli and Fonda 1979, Burge et al. 1980, Bradfield and Porter 1982, Dawe and White 1982 and 1986, Hutchinson 1982, Ewing 1983, Taylor 1983, Snow and Vince 1984, Bradfield and Campbell 1986, Campbell and Bradfield 1988).

Although *Salicornia virginica* and other true salt marsh species are subordinates or lacking in most Pacific Northwest marshes, these species often dominate in marshes lacking a continuous freshwater source (Ewing 1983). Few true salt marshes have been studied in the northwest. Kunze (1984) described ten such marshes in Washington, eight of which were less than 22 ha.

The Lake Hancock marsh, 15 km south of Coupeville on Whidbey Island (Fig. 1), despite its name, is actually a shallow, 15 ha lagoon surrounded by 69 ha of marsh (Fig. 2). The marsh is bounded by a *Pseudotsuga menziesii*/*Picea sitchensis* forest on the north, a mixed *Alnus rubra*/*Pseudotsuga menziesii*/*Picea sitchensis*/*Tsuga heterophylla* forest on the south, Washington Highway 20 on the east, and a baymouth bar to the west. Furthermore, many logs have accumulated

TABLE 2. Classification of North American Pacific coast marshes (from Macdonald 1977).

Coast Group	Latitude	Dominant Species
Arctic		
a) Arctic	71-69°	<i>Puccinellia phryganodes</i> <i>Stellaria humifusa</i>
b) Western Alaska	69-60°	<i>Carex subspathacea</i> <i>C. glarosa</i> ; <i>C. rariflora</i>
Subarctic (SE Alaska)	60-54°	<i>Puccinellia</i> spp. <i>Carex</i> spp. <i>Deschampsia caespitosa</i> <i>Potentilla pacifica</i> <i>Triglochin maritimum</i>
Temperate		
a) British Columbia	54-51°	<i>Carex lyngbyei</i> <i>Deschampsia caespitosa</i> <i>Festuca rubra</i>
b) Washington-Oregon	51-43°	<i>Carex lyngbyei</i> <i>Deschampsia caespitosa</i>
c) Northern California	43-38°	<i>Spartina foliosa</i> <i>Salicornia virginica</i> <i>Distichlis spicata</i>
d) Central California	38-35°	<i>Salicornia virginica</i> <i>Salicornia subterminalis</i> <i>Suaeda californica</i>
Dry Mediterranean	35-32°	<i>Batis maritima</i> <i>Festuca palmeria</i> <i>Salicornia bigelovii</i> <i>Monanthocloe littoralis</i>

along the northern border of the salt marsh (Fig. 2). One drainage channel ~20 m wide breaches the baymouth bar and connects the lagoon with Admiralty Inlet (Fig. 2). Another channel, on the north side, once breached the bar, but now only distributes water brought in by the main channel. The majority of the marsh receives fresh water from precipitation only; the southeast corner has a spring that dilutes the salinity of a small area.

In her cursory study of the Lake Hancock marsh, Kunze (1984) recognized a low marsh dominated by *Distichlis spicata* and *Salicornia virginica* and a high marsh dominated by *Agrostis alba* and *Distichlis spicata*. She reported interstitial water salinities of 22-46 ppt in the low marsh, values that were significantly higher than those of other Washington coastal marshes. No salinities were reported for the high marsh.

Lake Hancock and the surrounding land are part of a target range used by the U. S. Naval Air Station, Whidbey Island. Practice ammunition was

dropped on the marsh until 1972. Live ammunition was used during World War II, but its effect on the marsh is undiscernible today. Because this site is part of the Naval Base, civilian use has been restricted, and only trespassing hunters and fishers have intruded on the marsh.

Because the Lake Hancock marsh is an environment rare north of California, it was selected for further study to test the hypothesis that species are distributed along gradients of environmental factors through the marsh. We specifically sought answers to the following questions: 1) What is the range of each environmental factor operating in the marsh? 2) What species are present in the marsh, and are they distributed according to any environmental gradient? 3) Which combination of factors controls the vegetation pattern? 4) Is the Lake Hancock marsh more similar to the lagoonal marshes of California, or to the deltaic marshes of Oregon, Washington, British Columbia, and southeast Alaska?

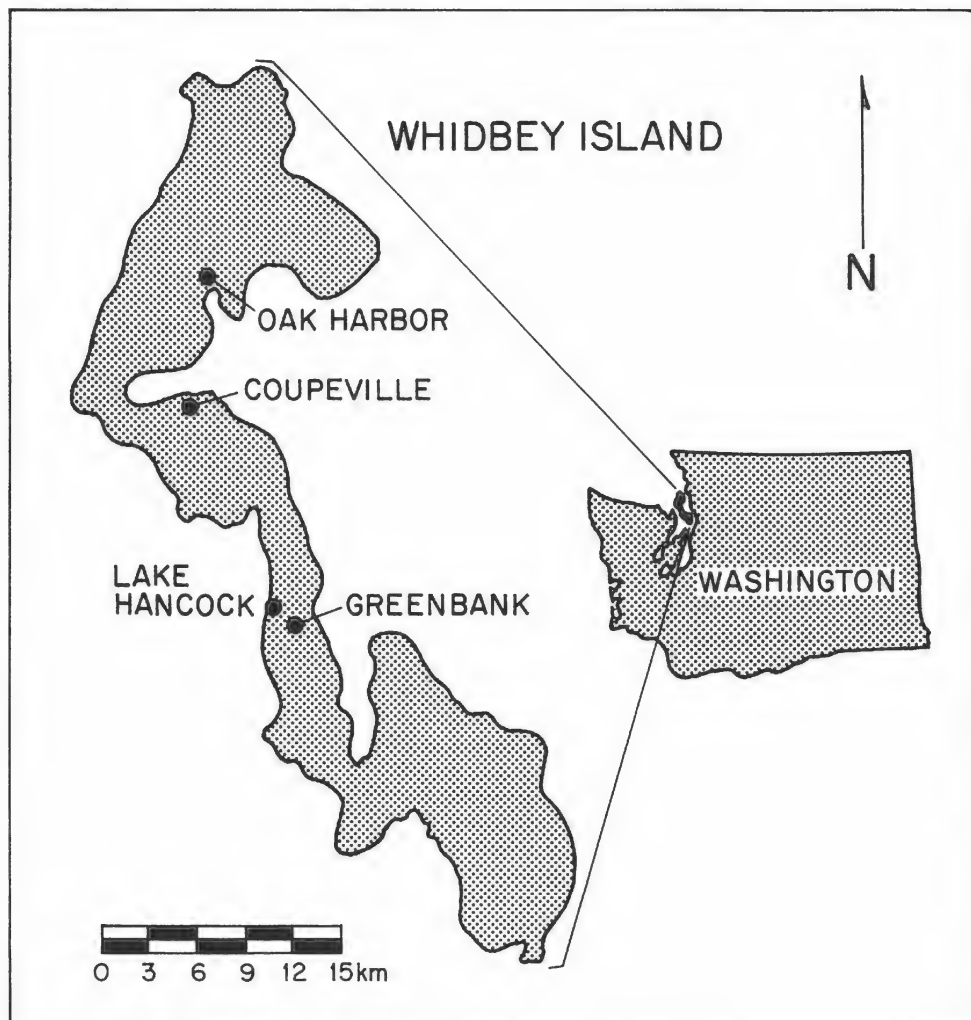


Figure 1. Location of Lake Hancock on Whidbey Island, Washington.

Methods

Five permanent transects perpendicular to the beachhead were established in the Lake Hancock marsh in June 1988 (Fig. 2). Site elevation is one of the most important environmental factors in marshes. While elevation itself has little effect on the vegetation, elevation does influence the environmental factors that are responsible for the vegetation zones. The marsh was surveyed by a team from the Public Works Department, U. S. Naval Air Station, Whidbey Island, using a Bausch

and Lomb Electronic Measuring System. Two permanent benchmarks located in the uplands adjacent to the northwest corner of the marsh were used for reference to position two temporary benchmarks in the marsh. Marsh elevations were measured to the temporary benchmarks every 10 m along the five transects. Elevations are accurate to 2.5 cm above mean lower low water.

Environmental factors were monitored every two weeks from 2 July to 24 September 1988 at 46 stations placed 40 m apart along the transects.

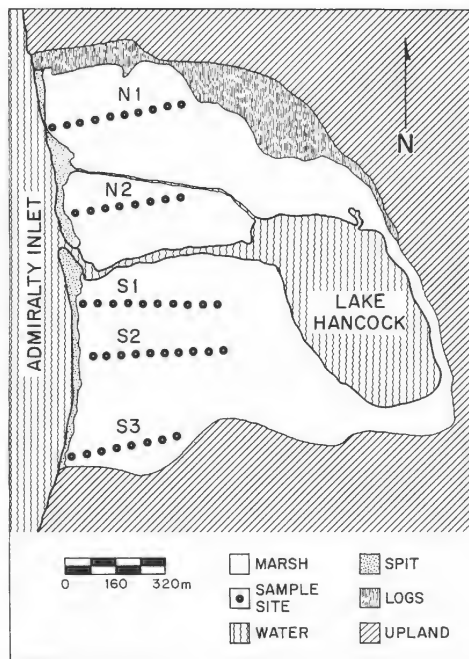


Figure 2. The study site and the transects along which all data were collected.

At each station, 100 cm of a 150 cm PVC pipe was left in the substrate to sample water table depth and salinity. The pipe had been capped and drilled with 6 mm holes along 9 cm of the inserted end for unrestricted water flow, and we assumed that water in the pipe would rise and fall with the water table. Such an arrangement insured that tide water would not cover the exposed end, and it provided ~90 cm of soil to act as a barrier to either rain water or tide water entering the pipe through the holes. Since we were uncertain how deep the water table could drop during the summer, we felt that the ~90 cm length insured that the water table would not drop below the reach of the pipes. Surface water salinity was measured in the middle of each transect at a site that had persistent surface water. Station 5 of each transect met this requirement. Water table depth was measured by inserting a rubber tube into the pipe until it contacted water. The tube then was removed and the length of the inserted section was measured. Water table samples were siphoned with the rubber tube from the PVC pipes. All salinities were measured with a temperature compensated Reichert opti-

cal salinometer. This instrument is accurate to 1‰ (Behrens 1965).

Soil samples weighing 500 g were taken from the root zone at each station on 13 Aug 1988. Samples were placed in storage bags and sealed to prevent water loss. The following day, soil moisture was determined on 125 g subsamples. These samples were dried at 105°C for 24 hr then reweighed. Soil moisture is expressed as percent of oven dry weight. Because soil factors remain relatively constant in lagoonal marshes (Barnes 1980), soil moisture was measured only once. The remaining soil was dried, mixed, and passed through a 2 mm sieve. We determined soil organic matter (as loss-on-ignition) by grinding 15 g samples with mortar and pestle, passing them through a 15 mm sieve, then firing them at 400°C for 8 hr. Soil clay content was determined on the 2 mm fraction by the Bouyoucos (1951) hydrometer method. The hydrometer samples were filtered through a 53 μ m sieve to determine sand content.

Vegetation was sampled in August, 1988, after all species had flowered and had been identified. Every 10 m along the transects, low-growing species within a 20 x 50 cm frame were scored for cover; tall species were scored within a 1 m radius plot. The cover classes of Daubenmire (1959) were used. Botanical nomenclature follows Hitchcock and Cronquist (1976).

The research was designed so that all statistical inferences made in the study could be based on a completely randomized design (ANOVA), using either the five transects or the various elevation classes as the treatments. Data also were compared to determine if significant correlations existed among the factors. The significance level was set at 5% before the research began.

Results

Elevation and Inundation

The Lake Hancock salt marsh increases in elevation with distance from Admiralty Inlet. The correlation between elevation and distance ($r=0.6$) was significant (Table 3). Elevations ranged between 32 cm and 129 cm above mean lower low water (MLLW) and were distributed normally. Mean sea level is 146.3 cm above MLLW, which places the entire Lake Hancock marsh below mean sea level. Mean low water (MLW) for Lake Hancock is 84.7 cm above MLLW; 43% of the study plots lie below MLW. Only elevations >55

TABLE 3. Correlation coefficients (r) for various marsh factors. Boldface numbers are significant.

	Water table salinity	Water table depth	Organic content	Sand content	Soil moisture	<i>Salicornia</i> cover	Bare ground	Distance from the inlet
Elevation	-0.4	0.1	0.4	-0.5	0.5	0.3	-0.3	0.6
Water table salinity		0.01	0.02	-0.01	0.01	0.03	0.02	0.7
Water table depth			0.1	0.01	-0.1	0.1	-0.2	-0.1
Organic content				-0.9	0.9	0.1	-0.2	0.9
Sand content					-0.9	0.1	0.4	-0.8
Soil moisture						0.6	-0.3	0.7
<i>Salicornia</i> cover							-	0.2
Bare ground								-0.3

cm above MLLW were vegetated. The elevations along transect N1 were significantly higher than the others, while those along transect N2 were significantly lower. Transects S1, S2, and S3 were not significantly different from each other (Fig. 2).

Despite these low elevations, parts of the marsh are not inundated every day. Because the marsh is connected to the ocean by only a narrow channel, flooding depends on the height of the previous low tide instead of the height of the incoming tide. Lower than average low tides allow excessive water to escape from the marsh. The narrow channel limits input, so that the subsequent high tide is unable to supply sufficient water to flood the marsh. Whenever the difference between one high tide and the subsequent low tide is >2 m, Lake Hancock continues to drain for up to 3 hr after the tide begins to rise again. Consequently, the entire marsh floods when there is little difference between the height of a high tide and the subsequent low tide, a situation that happens 30% of the time during the growing season. Otherwise, one tidal cycle lacks time to move enough water into the marsh to flood all sites.

The summer flooding pattern for the marsh is shown in Fig. 3. Sea water enters only through the main channel to fill the lake. Overflow then fills the closed channel and the log accumulation, and floods the eastern half of transect N1 and all of transect N2. On the south side, a system of channels carries the water along the bar and into the marsh, so that the first two stations of transects S1 and S2 flood at times. Transect S3 rarely floods during summer, because it lacks the channels that are common to transects S1 and S2. On the outgoing tide, the sea water drains back into the main

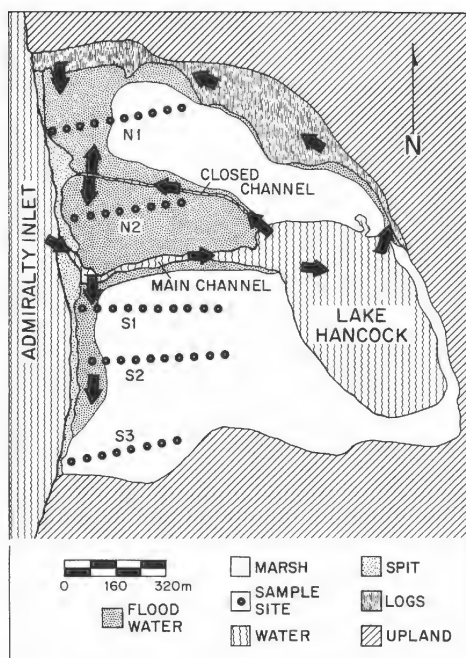


Figure 3. Summer flooding pattern of the Lake Hancock marsh.

channel. Because of the irregular flooding pattern in the marsh, the depth, duration, and number of days per year the marsh is flooded could not be calculated using existing computer programs.

Water Table Depth

Water table depths ranged from 0.4 cm to 21 cm (Table 4); mean depth was 11 cm. There were no significant differences among the transects or

TABLE 4. Mean water table depth (cm) and salinity (ppt), soil moisture (% dry weight), soil organic matter (% entire sample), soil texture (% mineral fraction) for each elevation class. Numbers in parentheses indicate the number of plots in each class.

	Elevation (cm)													
	32-37 (1)	44-49 (1)	56-61 (4)	62-67 (2)	68-73 (2)	74-79 (4)	80-85 (8)	86-91 (7)	92-97 (5)	98-103 (7)	104-109 (1)	110-115 (2)	116-121 (1)	129 (1)
Water table														
Depth	<1	5	3	5	4	21	15	21	13	13	14	15	13	11
Salinity	30	30	30	30	29	30	27	34	31	37	28	28	29	40
Soil moisture	59	426	138	257	270	213	317	178	345	355	400	270	300	355
Organic matter	6	57	30	43	45	34	47	28	51	61	78	50	56	65
Soil texture														
Sand	89	34	62	29	41	38	34	51	33	27	19	33	31	21
Silt	7	52	23	52	44	41	41	35	43	50	57	45	38	44
Clay	4	14	15	19	15	21	25	14	24	23	24	22	31	35

elevation classes. Water table depth failed to correlate significantly with any other variable in the study (Table 3).

Salinity

The Lake Hancock marsh is euhaline. Mean surface water salinities at individual stations ranged from 33-46 ppt. The surface water on seldom-flooded transect S3 was significantly more saline (46 ppt) than the surface water on the other transects. There were no significant differences in surface water salinity among the remaining transects.

Mean water table salinity was 31 ppt which is not significantly different from the salinity of Admiralty Inlet or of Lake Hancock. Salinities ranged from 27-40 ppt (Table 4). There were no significant differences in water table salinities among the transects or the elevation classes. Water table salinity correlated significantly with distance from the inlet (Table 3); as distance increased, salinity increased ($r = 0.7$).

Soil Factors

The soil moisture of the Lake Hancock marsh was high. Values ranged from 59-426% of dry weight (Table 4). Mean water content was 245%. There was a significant correlation between soil water and both elevation and distance from Admiralty Inlet (Table 3); as elevation or distance increased, soil water increased ($r = 0.5$ & 0.7). Soil water correlated positively with organic matter ($r = 0.9$)

and negatively with sand content ($r = -0.9$). Organic matter in soils increases the water holding capacity whereas sand increases drainage and decreases water holding capacity. Soils with a high organic matter to sand ratio will have higher soil moisture values.

The substrate of the Lake Hancock marsh is a Histosol. Organic content ranged from 6-78% with a mean of 46% (Table 4). There were no significant differences in organic matter content among transects, but the single site in the 32-37 cm elevation class had significantly less organic matter than did the other elevation classes. This site was closest to the sand bar, was regularly inundated, and was not vegetated, so that there was little opportunity for this site to accumulate organic material. Organic matter correlated significantly with elevation and with distance from the inlet (Table 3); as elevation or distance increased, organic matter increased ($r = 0.4$ & 0.9).

There were no significant differences in sand, silt, or clay content among transects or elevation classes (Table 4). Sand content correlated negatively with elevation, organic matter content, and distance from the inlet (Table 3). Sand content fell with increased elevation, organic matter, or distance.

Vegetation

Ten species were sampled in the marsh. *Salicornia virginica* dominated 82% of the vegetated plots, co-dominated on 11%, and was absent from 7%.

TABLE 5. Mean percent cover (C) and frequency (F) for species with >3% cover in at least one of the elevation classes. Plots below 56 cm were unvegetated. A total of 10 species occupied the marsh.

		Elevation (cm)										
		56-61 (7)	62-67 (6)	68-73 (6)	74-79 (20)	80-85 (25)	86-91 (33)	92-97 (20)	98-103 (19)	104-109 (4)	110-115 (7)	116-129 (5)
Species												
<i>Salicornia virginica</i>	C	18	48	35	63	92	55	61	61	48	57	50
	F	38	83	40	81	92	82	95	90	100	86	80
<i>Triglochin maritimum</i>	C				13	15	8	4	3			
	F	+	+	+	50	64	36	30	32	+	+	+
<i>Distichlis spicata</i>	C						3	4	3			
	F	-	-	-	+	+	58	20	16	+	+	-
<i>Jaumea carnosa</i>	C						3	3		10		
	F	+	-	-	+	+	21	25	+	25	-	-
<i>Potentilla pacifica</i>	C							4	5			
	F	-	-	-	-	+	-	10	5	-	-	-
Total species		4	3	2	5	7	5	9	7	4	4	1

+: <3% cover -: absent

Salicornia had moderate to high cover in all elevation classes, reaching peak cover in the 80-85 cm class (Table 5). *Salicornia* was distributed essentially continuously across the marsh.

There were no significant differences in *Salicornia* cover among transects or elevations. *Salicornia* cover correlated significantly with both elevation and soil moisture (Table 3); as elevation and soil moisture increased, *Salicornia* cover increased.

Triglochin maritimum was present in low cover and moderate frequency in all but two elevation classes (Table 5). It dominated 5% of the vegetated plots and co-dominated with *Salicornia* on 8%. In terms of elevation classes, however, it clearly was subordinate. There were no significant differences in *Triglochin* cover among transects or elevation classes. The distribution pattern is best described as patchy through the middle elevations.

Distichlis spicata and *Jaumea carnosa* were present at low cover and frequency (Table 5). They co-dominated with *Salicornia* on 3% of the vegetated plots; *Distichlis* and *Jaumea* each dominated 1% of the plots. Even when they were present,

their distribution was patchy at best. There were no significant differences in cover for any of these species among the transects or elevations.

Not shown in Table 5 is *Atriplex patula* var. *hastata*, which averaged 3% cover only for the 92-97 cm elevation. This species was distributed in small amounts throughout the marsh from 56 to 129 cm above MLLW.

Near the east end of transect S3, a fresh water spring diluted the environmental salinity to brackish conditions, which enabled *Potentilla pacifica* and *Typha latifolia* to occupy the site. *Salicornia* was absent here. Although both *Potentilla* and *Typha* had high cover on three sites, only *Potentilla* achieved more than 3% cover in one elevation class (Table 5). *Potentilla* and *Typha*, both common fresh water to brackish water marsh species, were an insignificant component of the Lake Hancock salt marsh.

Of greater significance, *Carex lyngbyei* and *Scirpus americanus*, indicator species of brackish conditions in most deltaic marshes between Oregon and Alaska, were absent from the Lake Hancock marsh.

TABLE 6. Mean percent cover for wood, ground, water, and plants for each elevation class. For those columns that do not sum to 100%, dead organic litter or other detritus accounted for the difference.

	Elevation (cm)														
	32-37	38-43	44-49	56-61	62-67	68-73	74-79	80-85	86-91	92-97	98-103	104-109	110-115	116-121	129
Wood	-	-	-	+	-	17	+	-	+	6	-	+	5	15	-
Ground	38	100	71	87	34	24	11	+	10	5	9	10	+	23	-
Water	38	-	29	-	11	33	-	5	11	+	13	25	5	+	-
Plants	-	-	+	21	49	35	76	108	70	80	73	58	61	50	88

+: <3% -: absent

The greatest species diversity was recorded from 80-103 cm above MLLW (7-9 species). Below or above these elevations only a handful of species were successful (Table 5).

Wood, bare ground, and water were present on 43% of the sample plots. Of the sites sampled in the marsh, 80% were vegetated. Ground or water covered 20%, most of which were <56 cm above MLLW. Wood had low cover at all elevations (Table 6); there were no significant differences in cover of wood among transects or elevations. Bare ground was present in all elevation classes, although the percent of bare ground was variable (Table 6). Transect N2, with its low elevations, had significantly more bare ground than the other transects, which were not significantly different from each other. Among elevation classes, there were no significant differences in percent cover for bare ground. Bare ground correlated negatively with elevation, soil water, and distance from the inlet, but positively with sand content (Table 3). Cover for water was low to moderate on all transects and in all elevation classes. There were no significant differences in water cover among transects or elevation classes.

Discussion

The Lake Hancock salt marsh was a single community dominated by the perennial chenopod *Salicornia virginica*; several other plant species were minor marsh components (Table 5). The arrangement of the data in Table 5 makes it seem that the minor plant species are limited to elevations between 74 cm and 109 cm. Their ranges are wider than that, however, but their cover values drop below 3%. For instance, *Triglochin maritimum* was distributed from 56 cm through 129 cm. The combined values for cover and frequency in Table 5 suggest, for the most part, that

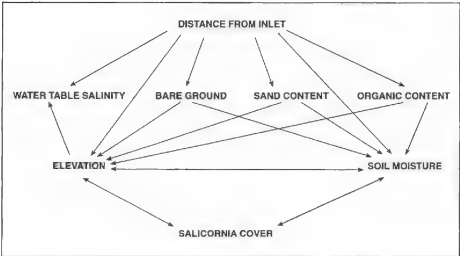


Figure 4. Significant interactions among the important environmental factors and *Salicornia* cover in the salt marsh. The arrows indicate the probable direction of the interaction. This diagram makes it clear that *Salicornia* cover is directly correlated with elevation and soil moisture, but that those two factors interact with five other factors to derive their ultimate effect.

the subordinate species in the salt marsh were distributed randomly.

The significant interactions that lead to the relationships among elevation, soil moisture, and *Salicornia* cover, relative to the hypothesis stated in the Introduction, are shown in Figure 4. The figure is based on the significant correlations among selected variables (Table 3), but it does not represent causal relationships. Nevertheless, it is clear that *Salicornia* cover is directly correlated with elevation and soil moisture, and that elevation and soil moisture are products of the interactions of the other factors. Although distance from the inlet has some of the highest correlation coefficients in Table 3, and specifically with *Salicornia* cover, its effects are manifested through the other environmental factors in the marsh.

Soil water indicates the degree to which a soil is aerated. *Salicornia* grows in pure stands on low elevation plots because such sites frequently are inundated and have highly saline, poorly aerated

substrates (Purer 1942, Hinde 1954, Chapman 1960, Vogl 1966, Eilers 1975, Burge et al. 1980, Kunze 1984, Dawe and White 1986). All sites in the Lake Hancock marsh were at low elevations. Although not all plots were flooded frequently, all had saline, hypoxic soils which allowed *Salicornia* to dominate. In other marshes, *Distichlis spicata* often was dominant to, or co-dominant with, *Salicornia* (Purer 1942, Hinde 1954, Chapman 1960, Kunze 1984). To outcompete *Salicornia*, however, *Distichlis* requires less saline, better aerated soils than were present in the Lake Hancock marsh.

Euhaline environments as extensive and accessible as the Lake Hancock marsh are rare north of Morro Bay, California. Kunze (1984) described nine other euhaline marshes in Washington, the largest of which was only 25% the size of the Lake Hancock marsh, and all were less accessible. Kunze (1984) incorrectly reported that at Lake Hancock the substrate was sand and *Distichlis* co-dominated with *Salicornia*.

Despite its north coast location, the Lake Hancock marsh lacks close floristic ties with the deltaic marshes of the Pacific Northwest. Numerous studies in Oregon (Eilers 1975, Jefferson 1975, Hutchinson 1982), Washington (Disraeli and Fonda 1979, Burge et al. 1980, Ewing 1983, Kunze 1984), British Columbia (Bradfield and Porter 1982, Dawe and White 1982 and 1986), and Alaska (Stephens and Billings 1967, del Moral and Watson 1978, Snow and Vince 1984, Vince and Snow 1984, Stone 1993) indicated that *Carex lyngbyei* dominated the majority of these brackish marsh environments. *Carex lyngbyei* was notably absent at Lake Hancock, because of the euhaline environment.

Salicornia virginica was reported on the delta of Eagle River, near Juneau, Alaska (Stone 1993). Because no quantitative data were given for *Salicornia* cover, its extent, elevation above MLLW, and the ranges of salinity across which it was found, it is impossible to compare data from Lake Hancock to Eagle River.

The Lake Hancock marsh more closely resembles the euhaline lagoonal marshes of central and southern California. The highest zone of the Newport marsh (Vogl 1966) compares well with the Lake Hancock marsh (Table 7). Vogl (1966) stated that *Salicornia virginica* had the broadest tolerance and was the most important species in the Newport marsh, a description that

TABLE 7. Comparison of mean percent cover of species important in the upper zone of the Upper Newport Bay marsh to those of the Lake Hancock marsh.

Species	Newport Bay	Lake Hancock
<i>Salicornia virginica</i>	40	52
<i>Triglochin maritimum</i>	1	7
<i>Distichlis spicata</i>	5	2
<i>Monanthocloe littoralis</i> *	15	-
<i>Scirpus californicus</i> *	14	-
<i>Jaumea carnosa</i>	+	2
<i>Typha latifolia</i>	+	+

* Not found north of California

+: <2 % -: absent

accurately applies to the Lake Hancock marsh. On the other hand, *Spartina foliosa* had high cover at lower elevations in the Newport marsh. *Spartina foliosa* is unreported north of California, although *Spartina alterniflora* has been introduced into several Washington estuaries, including Willapa Bay and Grays Harbor, and *Spartina townsendii* has been planted in Stillaguamish Bay (Macdonald 1977). If either of these grasses invades the Lake Hancock marsh, it could become a significant component at lower elevations, resulting in a vegetation pattern almost identical to that of the lagoonal marshes of central and southern California.

Vogl (1966) measured no environmental factors at Newport Bay. The marshes of Newport Bay are similar to those in San Diego County (Vogl 1966), where Purer (1942) did measure salinity. During the growing season, mean maximum salinities for San Diego sites that regularly were connected with the ocean ranged from 30-48 ppt, values that compare closely to the mean of the maximum salinities measured at each environmental station at Lake Hancock (33 ppt).

Callaway et al. (1990) focused heavily on soil salinity as a factor governing vegetation pattern at the Carpinteria marsh. Comparisons between Lake Hancock and Carpinteria are tenuous, largely because Lake Hancock lies entirely below mean sea level whereas the lowest elevations for the Carpinteria study were 85 cm above mean sea level. Nevertheless, the low marsh zone at Carpinteria, dominated by *Salicornia virginica* was high in salinity throughout the year. Water table salinity at Lake Hancock remained high throughout the summer, and we have no doubt

that the daily inundation by sea water maintains that situation throughout the year.

To date there have been no published reports of euhaline marshes in either British Columbia or Alaska. The Lake Hancock marsh appears to be the northernmost euhaline marsh on the Pacific coast. All other sizable marshes north of California are brackish marshes, not true salt marshes. This fact is supported not only by environmental data, but also by the predominance of *Carex lyngbyei* and other brackish marsh species (Crow 1977). The Lake Hancock marsh is a unique environment and it warrants further study in all areas.

Literature Cited

- Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44:445-456.
- Barnes, R. S. K. 1980. Coastal Lagoons: the Natural History of a Neglected Habitat. Cambridge University Press, Cambridge.
- Behrens, E. W. 1965. Use of the Goldberg refractometer as a salinometer for biological and geological field work. *J. Mar. Res.* 23:165-171.
- Bertness, M. D. and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.* 52:129-147.
- Blum, J. L. 1968. Salt marsh *Spartinas* and associated algae. *Ecol. Monogr.* 38:199-221.
- Bouyoucos, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soil. *Agron. J.* 43:434-438.
- Bradfield, G. E. and A. Campbell. 1986. Vegetation-elevation correlation in two dyked marshes of northeastern Vancouver Island: multivariate analysis. *Can. J. Bot.* 64:2487-2494.
- Bradfield, G. E. and G. L. Porter. 1982. Vegetation structure and diversity components of a Fraser estuary tidal marsh. *Can. J. Bot.* 60:440-451.
- Burge, M. E., D. R. Tripp, and E. S. Rosenburg. 1980. Plant associations and primary production of the Nisqually salt marsh on southern Puget Sound, Washington, USA. *Northw. Sci.* 54:222-236.
- Callaway, R. M., S. Jones, W. R. Ferren, and A. Parikh. 1990. Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distribution and soil salinity in the upper marsh. *Can. J. Bot.* 68: 1139-1146.
- Campbell, A. and G. E. Bradfield. 1988. Comparison of plant community-environment relations in two estuarine marshes of northern British Columbia. *Can. J. Bot.* 67:146-155.
- Chapman, V. J. 1940. Succession on the New England salt marshes. *Ecology* 21:279-282.
- _____. 1960. Salt Marshes and Salt Deserts of the World. Interscience Publishers, Inc. New York.
- _____. 1976. Coastal Vegetation (2nd ed.). Macmillan Co., New York.
- Conard, H. S. 1924. Second survey of vegetation of a Long Island salt marsh. *Ecology* 10:326-336.
- Crow, J. H. 1977. Salt marshes of the Alaska Pacific coast. P. 103-109 in R. D. Andrews, R. L. Carr, F. Gibson, B. Z. Lang, R. A. Soltero, and K. C. Swedberg (eds.), Proceedings of the Symposium on Terrestrial and Aquatic Ecological Studies of the Northwest. Eastern Washington State College Press, Cheney, Washington.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northw. Sci.* 33:43-64.
- Dawe, N. K. and E. R. White. 1982. Some aspects of the vegetation ecology of the Little Qualicum River estuary, British Columbia. *Can. J. Bot.* 60:1447-1460.
- _____. 1986. Some aspects of the vegetation ecology of the Nanoose Bonnell estuary, Vancouver Island, B. C., Canada. *Can. J. Bot.* 64:27-34.
- del Moral, R. and A. F. Watson. 1978. Vegetation of the Stikine flats, southeast Alaska. *Northw. Sci.* 52:137-150.
- Disraeli, D. J. and R. W. Fonda. 1979. Gradient analysis of the vegetation in a brackish marsh in Bellingham Bay, Washington. *Can. J. Bot.* 57:465-475.
- Eilers, H. P. 1975. Plants, plant communities, net production, and tide levels: the ecological biogeography of the Nehalem salt marshes, Tillamook County, Oregon. Ph. D. Dissertation, Oregon State University, Corvallis.
- Ewing, K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. *Can. J. Bot.* 61:1105-1116.
- Ganong, W. F. 1903. The vegetation of the Bay of Fundy salt and diked marshes: an ecological study. *Bot. Gaz.* 36:161-186.
- Glooschenko, W. A. 1980. Coastal marshes of Canada. P. 39-47 in E. C. A. Rubec and F. C. Pollett (eds.), Proceedings of a Workshop on Canadian Wetlands. Environment Canada Lands Directorate, Ecological Lands Classification Series No. 12.
- Hartman, J. M. 1988. Recolonization of small disturbance patches in a New England salt marsh. *Amer. J. Bot.* 75:1625-1631.
- Hinde, H. P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide levels. *Ecol. Monogr.* 24:209-225.

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- Hitchcock, C. L. and A. Cronquist. 1976. Flora of the Pacific Northwest. University Washington Press, Seattle.
- Hutchinson, I. 1982. Vegetation-environment relations in a brackish marsh, Lulu Island, Richmond, B. C. Can. J. Bot. 60:452-462.
- Jefferson, C. 1975. Plant communities and succession in Oregon coastal salt marshes. Ph. D. Dissertation, Oregon State University, Corvallis.
- Kunze, L. M. 1984. Puget Trough Coastal Wetlands. A Summary Report of Biologically Significant Sites. Washington Department of Natural Resources, Natural Heritage Program, Olympia, for the Washington Department of Ecology.
- Macdonald, K. B. 1977. Plant and animal communities of Pacific North American salt marshes. P. 167-192 in V. J. Chapman (ed.), Ecosystems of the World. Vol. I: Wet Coastal Ecosystems. Elsevier Scientific Publishing Co., Amsterdam.
- Miller, W. R. and F. E. Egler. 1950. Vegetation of the West Quetequock-Pawcatuck tidal marshes, Connecticut. Ecol. Monogr. 20:143-172.
- Newby, L. C. 1982. Salt marsh coasts. P. 706-708 in M. L. Schwartz (ed.), The Encyclopedia of Beaches and Coastal Environments. Hutchinson Ross Publishing Co., Stoudsburg, Pennsylvania.
- Nixon, S. W. and C. A. Oviatt. 1973. Ecology of a New England salt marsh. Ecol. Monogr. 43:463-498.
- Penfound, W. T. 1952. Southern swamps and marshes. Bot. Rev. 18:413-446.
- Purer, E. A. 1942. Plant ecology of the coastal marshes of San Diego County, California. Ecol. Monogr. 12:81-111.
- Ranwell, D. S. 1972. Ecology of Salt Marshes and Sand Dunes. Chapman and Hall, London.
- Redfield, A. C. 1965. The ontogeny of a salt marsh estuary. Science 147:50-55.
- . 1972. Development of a New England salt marsh. Ecol. Monogr. 43:201-237.
- Reimold, R. J. 1977. Mangals and salt marshes of the eastern United States. P. 157-166 in V. J. Chapman (ed.), Ecosystems of the World. Vol. I: Wet Coastal Ecosystems. Elsevier Scientific Publishing Co., Amsterdam.
- Snow, A. A. and S. W. Vince. 1984. Plant zonation in an Alaskan salt marsh II: an experimental study of the role of edaphic conditions. J. Ecol. 72:669-684.
- Stephens, F. R. and R. F. Billings. 1967. Plant communities of a tide influenced meadow on Chichagof Island, Alaska. Northw. Sci. 41:178-183.
- Stone, C. S. 1993. Vegetation of coastal marshes near Juneau, Alaska. Northw. Sci. 67: 215-230.
- Taylor, A. H. 1983. Plant communities and elevation in a diked intertidal marsh in the Coos Bay estuary, Oregon. Northw. Sci. 57:132-142.
- Teal, J. M. 1961. Gas exchange in a Georgia salt marsh. Limnol. and Oceanogr. 6:388-394.
- . 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.
- Udell, H. G., J. Zarudsky, and T. E. Doheny. 1969. Productivity and nutrient values of plants growing in the salt marshes of the town of Hempstead, Long Island. Bull. Torrey Bot. Club 96:42-51.
- Vince, S. W. and A. A. Snow. 1984. Plant zonation in an Alaskan salt marsh I: distribution, abundance, and environmental factors. J. Ecol. 72:651-668.
- Vogl, R. J. 1966. Salt marsh vegetation of upper Newport Bay, California. Ecology 47:80-87.

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and

Analysis of the Associations between Macroinvertebrates and Macrophytes in a Freshwater Pond

Abstract

The interactions between aquatic macrophytes and macroinvertebrates are complex, with macrophytes often providing both refuge and food, either directly or indirectly, for invertebrates. Macroinvertebrate-plant relationships have been studied extensively in terrestrial environments, but much less so in aquatic environments. The objective in this paper was to explore some of the factors that affect macroinvertebrate-macrophyte relationships in the littoral zone of a freshwater pond. A total of 53 macroinvertebrate taxa were found associated with six macrophyte species in Cannery Pond, a small, shallow, eutrophic pond in Skagit Co., WA (USA). A graphical inspection of the data revealed that the macroinvertebrate densities and biomasses on the emergent macrophyte species (*Scirpus tabernaemontani*, *Typha latifolia*, and *Polygonum hydropiperoides*) were more similar to each other than to the submerged macrophyte species (*Potamogeton natans*, *Ceratophyllum demersum*, and *Potamogeton pusillus*). Multivariate analyses (MANOVA) confirmed that there were significant differences among the plant taxa based on macroinvertebrate densities and biomasses. Cluster analyses (parametric and nonmetric) further revealed that the strongest grouping was into two groups (emergent and submerged plants) rather than the original six. The greatest differences between submerged and emergent plants were due to differences in the abundances of Mollusca, Annelida, Platyhelminthes, Crustacea and Diptera, all of which were common taxa. Morphological similarities among plants appeared to influence macroinvertebrate-macrophyte associations, with the greatest abundances of macroinvertebrates being found on submerged plants that had a large surface-to-weight ratio and soft stems or leaves. Structural stability and persistence of vegetative structures throughout the year appear to be important for at least some of the macroinvertebrates. Most of the macroinvertebrate taxa in Cannery Pond were substrate generalists that are not confined to a particular species of macrophyte, but instead were found in similar abundances on all morphologically similar macrophytes.

Introduction

Macrophytes are an important component for macroinvertebrates in freshwater lakes because they may serve as a refuge from predators (Gilinsky 1984, Brown et al. 1988, Hargeby 1990), substrate, allowing macroinvertebrates to utilize a greater portion of the water column (Soszka 1975, Rabe and Gibson 1984), indirect food sources for grazing and scraping organisms that feed on surficial Aufwuchs (Rabe and Gibson 1984, Hargeby 1990), and direct food sources for mining and shredding macroinvertebrates (Newman 1991). Most aquatic macroinvertebrates show some type of substrate association or "preference" (Minshall 1984). In lentic environments, aquatic macrophytes generally support a higher density of macroinvertebrates than other types of substrates. The greatest macroinvertebrate densities are usually found in vegetated areas that are structurally heterogeneous, (Voigts 1976, Murkin and Batt 1987, Brown et al. 1988), on plants that have a large surface area, (Dvorak and Best 1982, Findlay et

al. 1989, Chilton 1990), and in vegetation that covers a large spatial area or persists throughout winter (Minshall 1984, Sweeney 1984). The macrophyte features that appear to influence macroinvertebrate species richness are patch size and seasonal persistence of vegetative structures, the heterogeneity and texture of the plant surface, macrophyte surface area and the degree of leaf dissection, the position of the plant in the water column, the degree of microbial surface growth, and the amount of silt or organic matter that accumulates on the plant surfaces (Biochino and Biochino 1979, Minshall 1984, Downing 1986, Murkin and Batt 1987, Schramm et al. 1987, Wrubleski 1987, Chilton 1990).

Our research objective was to look for differences in macroinvertebrate composition and abundance on different macrophytes in the littoral zone of a freshwater pond. The scope of this objective clearly exceeds our single-season research effort. Still, data from community-level, multi-species studies are needed in order to make generalizations

about the nature of macroinvertebrate associations with aquatic plants. With this in mind, we sampled six common emergent and submerged macrophyte species in Cannery Pond, a small (1 ha), shallow (maximum depth < 1.5 m), eutrophic freshwater pond near Anacortes, Washington (Parsons 1992). The sediments consist of a thick layer (> 60 cm) of decaying organic matter. Vegetation in the pond includes extensive floating mats of *Typha latifolia* L. (common cat-tail) and outcroppings of *Scirpus tabernaemontani* K. C. Gmel. (great or soft-stem bulrush) that extend up to 60 m out from the shore. Submerged vegetation is mostly *Ceratophyllum demersum* L. (common hornwort) and *Potamogeton pusillus* L. (pondweed), that covers the pond bottom in open water areas, and *Potamogeton natans* L. (broad-leaved pondweed) and *Polygonum hydropiperoides* Michx. (waterpepper) in the transition zone between the emergent plants and open water (Parsons 1992). Our hypothesis was that there were significant differences among the macroinvertebrate assemblages associated with the different macrophyte species.

Materials and Methods

Macrophyte samples from *S. tabernaemontani*, *T. latifolia*, *P. hydropiperoides*, *C. demersum*, *P. pusillus*, and *P. natans* were collected on 14 July, 3 August, 24 August, and 29 September 1990 using a method similar to that described by Schramm et al. (1987). Three replicate macrophyte samples of at least 70 g wet weight were collected on each sample date (except 29 September) from nearly monospecific stands. On 29 September *P. pusillus* could not be collected because only a few small patches remained. All samples were collected using a 0.5 mm mesh net connected to a 0.1 m square metal frame. For the emergent plants (*S. tabernaemontani*, *T. latifolia*, and *P. hydropiperoides*), we collected only the portion of plant that was in the water column. For *T. latifolia*, the suspended root mass also was included in the sample. The submerged and floating-leaved plants (*P. natans*, *C. demersum*, and *P. pusillus*) were gathered into the net in their entirety. Macroinvertebrates were dislodged by squirting the plants with water; the plant material also was examined, and any remaining macroinvertebrates were removed. The wash water was strained through a 0.5 mm mesh and the resulting macroinvertebrate sample was preserved in 5% formalin or 70% ethanol.

All of the collected macrophyte samples were blotted dry and weighed to the nearest 0.1 g to determine wet weight. Macrophyte subsamples were collected to determine dry weight, ash-free dry weight, and surface area conversion factors. An electronic planimeter was used to measure the surface area of photocopied images of submersed portions of preweighed, flat-leaved plant specimens. Geometric methods were used to estimate the surface area of cylindrical specimens. Samples from each macrophyte species were dried (48 hr at 100°C), composited by species, and subsamples of the dried material were ashed (6 hr at 550°C) to estimate dry weight and ash-free dry weight coefficients (APHA 1989).

Macroinvertebrates were identified to the lowest practical taxonomic level and quantified by number and biomass. To estimate biomass, all macroinvertebrates, except Odonata taxa, were separated into three size classes using sieves with a 1 mm and 2 mm mesh following the method described by Reger et al. (1982). A subsample of 10 individuals from each taxon (and size class, if appropriate) was dried to achieve an average dry weight (4 hr at 100°C) and an average ash-free dry weight (2 hr at 550°C) per individual. In cases of rare taxa, smaller subsamples were used. Due to their delicate nature, the Odonata taxa were counted, then measured for body length and head capsule width. A subsample of at least 10 different sized animals from each of the three common Odonata taxa was measured, dried, and weighed, then ashed and weighed to extrapolate dry weight and ash-free dry weight. Linear regression was used to estimate the dry weights and ash-free dry weights from length measurements of each Odonatan. A complete description of the conversions was provided by Parsons (1992). Dry weight and ash-free dry weights were correlated for all macroinvertebrate taxa ($r^2 = 0.98-99$; $p < 0.0001$), so we will report only the results for macroinvertebrate numerical abundances and ash-free dry weights, standardized by plant wet weight.

The data were evaluated using MANOVA and hierarchical clustering (SPSS, Inc. 1988). In addition, the data were clustered using RIFFLE, a nonmetric, nonparametric, clustering and association analysis procedure (Matthews and Hearne 1991, Matthews et al. 1995). Conventional clustering creates distance measures for each sample that incorporate all measured variables; "good" clusters are formed when groups of samples

have less intracluster distances than intercluster distances. By contrast, RIFFLE uses an iterative search to assign samples to clusters that have the most features in common, where a feature would be any measured quality such as "high/low" or "present/absent" or "red/blue." For example, one cluster might include all plant samples that had high densities of macroinvertebrates *A* and *B*, while another cluster might include samples that had low densities of *B* and *C* and high densities of *A*. The RIFFLE search procedure seeks to maximize the "proportional reduction in error," which is a measure of improvement in predicting feature values (over random guessing) that is provided by knowing a sample's cluster identity. Nonmetric clustering does not base clustering on preassigned group identities, so the RIFFLE program also includes an association analysis that indicates whether the nonmetric clusters are similar to known groups.

The SPSS-X multivariate procedures required collapsing the macroinvertebrate data into fewer taxonomic groups in order to reduce the number of zeros in the data set. We chose to use the following eleven categories: Ephemeroptera, Odonata, Hemiptera, Trichoptera, Coleoptera, Diptera, Mollusca, Annelida, Platyhelminthes, Crustacea, and "Other" (Collembola, Orthoptera, Lepidoptera and Arachnida-Hydracarina). The nonmetric clustering tests required equal numbers of plant groups; this caused omission of September data because *P. pusillus* could not be sampled at that time. For comparison, most of the statistical results presented here are for the July-August data, using the eleven macroinvertebrate categories. Where appropriate, the results were confirmed using the full taxo-

nomic data set and the July-September data, and any major differences were reported.

Results

Table 1 shows the average conversion factors from macrophyte wet weight to dry weight, ash-free dry weight, and surface area. *Scirpus tabernaemontani* had the highest conversion factors for dry weight and ash-free dry weight to wet weight, and the lowest conversion factor for surface area to plant wet weight. *Potamogeton pusillus* had the lowest conversion factors for dry weight and ash-free dry weight to wet weight, while *C. demersum* had the highest conversion factor for surface area to plant wet weight.

Fifty-three macroinvertebrate taxa were found associated with the six macrophyte species (the complete taxonomic list is available from the authors). Tables 2-3 show the average number and biomass (ash-free dry wt) of macroinvertebrates on each macrophyte species by plant wet weight and plant surface area. The three emergent species (*P. hydropiperoides*, *S. tabernaemontani*, and *T. latifolia*) supported relatively few macroinvertebrates, both in number and total biomass, per kg of macrophyte wet weight and per m² of plant surface area (*T. latifolia* surface area was not calculated due to the morphologically complex, suspended root masses). *Potamogeton pusillus* and *P. natans* had the greatest number and biomass of macroinvertebrates per kg of macrophyte wet weight and per m² of plant surface area. *Ceratophyllum demersum* supported a relatively large number and biomass of macroinvertebrates per kg of plant wet weight, but was similar to the emergents when compared using plant surface area.

TABLE 1. Macrophyte conversion factors.

Macrophyte	Average dry wt/wet wt	Average ash-free dry wt/dry wt	Average surface area to plant wet wt (m ² /kg)
<i>Scirpus tabernaemontani</i> (E)*	0.164	0.9462	1.42
<i>Typha latifolia</i> (E)	0.128	0.9294	na**
<i>Polygonum hydropiperoides</i> (E)	0.148	0.9388	4.47
<i>Potamogeton natans</i> (S)	0.130	0.9174	4.71
<i>Ceratophyllum demersum</i> (S)	0.127	0.8748	6.91
<i>Potamogeton pusillus</i> (S)	0.068	0.8501	4.62

*E = emergent; S = submerged; **Surface area of root mat was not measured.

TABLE 2. July-September average macroinvertebrate densities (#/kg wet wt plant) for six macrophyte species.

Macroinvertebrate Categories	Emergent Macrophyte Species			Submerged Macrophyte Species		
	<i>P. hydrop.</i>	<i>S. tabern.</i>	<i>T. latifolia</i>	<i>P. pusillus</i>	<i>P. natans</i>	<i>C. demersum</i>
Ephemeroptera	5 (15)*	16 (26)	6 (10)	0 (0)	13 (23)	2 (3)
Odonata	221 (178)	48 (39)	165 (178)	128 (98)	186 (152)	114 (94)
Hemiptera	0 (2)	1 (2)	2 (5)	1 (2)	14 (15)	0 (1)
Trichoptera	8 (16)	15 (20)	1 (2)	68 (93)	97 (139)	15 (23)
Coleoptera	27 (26)	5 (8)	12 (16)	12 (19)	12 (14)	6 (10)
Diptera	324 (245)	144 (85)	233 (128)	2674 (2557)	1160 (1022)	431 (275)
Mollusca	818 (505)	175 (187)	154 (99)	4091 (1070)	1260 (678)	2814 (1852)
Annelida	74 (79)	87 (152)	29 (43)	431 (311)	194 (91)	447 (559)
Platyhelminthes	171 (121)	98 (141)	53 (57)	598 (696)	874 (744)	309 (423)
Crustacea	1372 (746)	953 (685)	1016 (1006)	4703 (3220)	4626 (3189)	1882 (997)
Other	15 (11)	8 (8)	7 (10)	20 (14)	36 (48)	26 (62)
Total #/kg wet wt plant	3035 (1050)	1551 (1149)	1679 (1278)	12726 (5440)	8473 (4005)	6046 (2558)
Total #/m ² plant surface area**	679 (235)	1093 (809)	na	2754 (1178)	1799 (850)	875 (370)
Total taxa***	33	36	42	29	36	21

*Standard deviations are shown in parentheses for each mean value.

**Total #/m² plant surface area was calculated using the appropriate correction factors listed in Table 1.

***Total number of taxa collected on each plant species during July-September sampling period.

TABLE 3. July-September average macroinvertebrate biomass (mg/kg wet wt plant) for six macrophyte species.

Macroinvertebrate Categories	Emergent Macrophyte Species			Submerged Macrophyte Species		
	<i>P. hydrop.</i>	<i>S. tabern.</i>	<i>T. latifolia</i>	<i>P. pusillus</i>	<i>P. natans</i>	<i>C. demersum</i>
Ephemeroptera	1 (3)*	3 (5)	1 (1)	0 (0)	2 (4)	0 (1)
Odonata	289 (258)	70 (119)	201 (255)	83 (81)	182 (153)	131 (217)
Hemiptera	0 (0)	5 (16)	0 (1)	0 (0)	34 (114)	10 (34)
Trichoptera	17 (59)	9 (28)	0 (0)	17 (36)	7 (10)	1 (2)
Coleoptera	36 (50)	3 (6)	15 (19)	25 (45)	95 (161)	8 (13)
Diptera	13 (10)	9 (7)	13 (10)	158 (147)	77 (70)	31 (22)
Mollusca	198 (166)	54 (53)	38 (21)	766 (329)	488 (249)	557 (300)
Annelida	9 (9)	23 (28)	6 (7)	13 (9)	108 (68)	24 (18)
Platyhelminthes	18 (12)	11 (17)	6 (6)	66 (69)	100 (79)	38 (49)
Crustacea	66 (38)	41 (26)	89 (75)	256 (118)	234 (107)	134 (71)
Other	1 (1)	0 (0)	1 (3)	1 (1)	1 (1)	2 (4)
Total mg/kg wet wt plant	648 (337)	229 (167)	371 (325)	1384 (373)	1329 (505)	936 (365)
Total mg/m ² plant surface area**	145 (337)	161 (118)	na	300 (81)	282 (107)	135 (53)
Total taxa***	33	36	42	2	36	21

*Standard deviations are shown in parentheses for each mean value.

**Total mg/m² plant surface area was calculated using the appropriate correction factors listed in Table 1.

***Total number of taxa collected on each plant species during July-September sampling period.

The densities of Trichoptera, Diptera, Mollusca, Annelida, Platyhelminthes, and Crustacea usually were higher on the submerged plants than on emergent plants (Table 2). Within the submerged plant group, Trichoptera, Diptera, Crustacea, and Platyhelminthes were more numerous on *P. pusillus* and *P. natans* than on *C. demersum*. The ash-free dry weight biomass of the Diptera, Mollusca, Platyhelminthes, and Crustacea were greater on submerged plants, especially on *P. pusillus* and *P. natans* than on emergents (Table 3). Overall, the most numerous groups, based on equal weights of each plant, were Crustacea (dominated by *Hyalella azteca*), Mollusca (dominated by *Gyraulus*), and Diptera (dominated by Chironomidae). The order of dominance changed when ranked by biomass to: Mollusca (*Anodonta* and *Gyraulus*), Crustacea (*H. azteca*), and Odonata (*Enallagma*).

Polygonum hydropiperoides yielded the largest number and highest biomass of Odonata of all six macrophyte species, as well as relatively large numbers of Coleoptera, Diptera, Mollusca, Platyhelminthes, and Crustacea compared to the other emergent plant species. It supported 33 macroinvertebrate taxa. *Polygonum hydropiperoides* was the only macrophyte that contained the relatively rare Lepidopteran, *Acentria* (Other). *Scirpus tabernaemontani* supported a total of 36 taxa, and had more Ephemeroptera, Trichoptera, and Hirudinea (Annelida) than the other emergent taxa, but had relatively low densities of Odonata, Coleoptera, and Diptera. *Typha latifolia* had the greatest densities of *Asellus* and *Synurella* (Crustacea) and the second highest biomass of Odonata of all the macrophyte species; however, it had the lowest densities of Annelida and Platyhelminthes of the emergent taxa. Although *T. latifolia* had the second lowest total macroinvertebrate number (1679/kg plant wet wt) and biomass (371 mg/kg plant wet wt), it supported the largest number of macroinvertebrate taxa (42).

Both species of *Potamogeton* had the highest densities for many of the macroinvertebrate categories. Of the six plant species, *Potamogeton pusillus* contained the greatest total number and biomass of macroinvertebrates per plant, probably because it had the greatest number and biomass of Diptera and Mollusca. However, it had the lowest taxonomic richness (29 taxa). Miss-

ing taxa that were present on all other plants sampled included Ephemeroptera, Hirudinea (Annelida), and Collembola (Other). By contrast, *Chaoborus* (Diptera) was found only on *P. pusillus*.

Potamogeton natans had the second highest total macroinvertebrate density and biomass, the greatest density of Hemiptera, Trichoptera, and Platyhelminthes, and the second highest density of Crustacea. *Potamogeton natans* yielded a total of 36 taxa and had the only specimens of *Donacia* (Coleoptera) and most of the *Mesovelina* (Hemiptera), *Agraylea* (Trichoptera), Empididae, Ceratopogonidae (Diptera), Sciomyzidae (Diptera), and *Helobdella* (Annelida). It also showed the most evidence of destruction by macroinvertebrates; many of the leaves nearly were destroyed from tunnels made by mining organisms.

Ceratophyllum demersum had the highest surface-area-to-weight ratio (Table 1), but contained the lowest density and biomass of macroinvertebrates per kg of plant of all the submerged species. As a result, *Ceratophyllum* had the lowest density and weight of macroinvertebrates per unit area of plant surface of any of the submerged species. Although *Ceratophyllum* supported a relatively low number of taxa (32), it yielded large numbers of Mollusca (especially *Lymnaea*) and Oligochaeta.

Based on the 11 macroinvertebrate categories as test variables, and the MANOVA test, significant differences were found among the macroinvertebrate assemblages associated with the six plant species for both macroinvertebrate density and biomass data (Table 4). Similar results were obtained for both the July-September and July-August data. Furthermore, there were consistent, significant differences among the plant species for Odonata, Diptera, Mollusca, Annelida, Platyhelminthes, and Crustacea (ANOVA, $\alpha \leq 0.05$ for both biomass and density). Hemiptera and Trichoptera had significantly different densities, but not biomass, among the plant species (ANOVA, $\alpha \leq 0.05$); while Ephemeroptera, Coleoptera, and "Other" were not significantly different, using either density or biomass data.

The best parametric clustering results were obtained using Ward's method (minimum variance clustering) with a squared Euclidean distance measure (Figure 1). As with MANOVA, parametric clustering required condensing the macroinvertebrate data into 11 categories. There

TABLE 4. MANOVA results for 6 plant species and 11 macroinvertebrate categories.*

MANOVA based on macroinvertebrate densities (#/kg wet wt plant)					
Test name	Value	F**	Hypoth. DF	Error DF	Sig. of F.
Pillai's trace	2.299	3.250	55	210	< 0.001
Hotelling's trace	13.048	8.635	55	182	< 0.001
Wilkes' λ	0.013	5.076	55	179	< 0.001
Roy's largest root	0.911				
MANOVA based on macroinvertebrate biomass (mg/kg wet wt plant)					
Test name	Value	F**	Hypoth. DF	Error DF	Sig. of F.
Pillai's trace	2.283	3.207	55	210	< 0.001
Hotelling's trace	18.067	5.339	55	182	< 0.001
Wilkes' λ	0.022	4.204	55	179	< 0.001
Roy's largest root	0.830				

*July-August samples only.

**F is accurate to 3 decimal places (SPSS, Inc. 1988).

were two dominant clusters in the macroinvertebrate density data that separated most of the submerged and emergent macrophytes. The first cluster contained 32 of the 54 macrophyte samples, including 26 emergent samples and 6 submerged samples. The second cluster contained 22 samples (1 emergent + 21 submerged). The biomass data displayed a similar pattern, with all of the emergent samples in one cluster (27 emergent + 5 submerged); and most of the submerged samples in a second cluster (19 submerged). A third cluster appeared in the biomass data that consisted of three submerged samples. A close examination of the raw data showed no obvious similarity between these three samples other than their collection date (24 Aug).

Nonmetric clustering and association analysis (RIFFLE) provided results that were similar to the parametric tests: macroinvertebrate data were clustered into groups that were associated with the different plant species, and the clustering was better for two groups than for six groups. Table 5 presents RIFFLE results for the 55-taxa density data; similar results were obtained using the 55-taxa biomass data and both of the 11-category data files. For 2-group clusters, the RIFFLE proportional reduction of error was 49% (both density and biomass data), which means that by knowing the RIFFLE cluster assignment we can make a 49% better than random prediction of the biomass or density for the macroinvertebrate taxa. The 6-group clusters had a proportional reduc-

tion of error of 38% for density data and 41% for biomass data. Table 5 also shows which clusters were assigned to each plant sample. Most of the 6-group misclassifications were into a similar emergent or submerged group: groups 1, 3, and 6 contained 21 of the 27 emergent samples, and groups 1, 4, and 5 contained 22 of the submerged samples. RIFFLE made very few misclassifications for 2-group clustering.

One of the features of RIFFLE is to identify which variables were most important in generating clusters. As with MANOVA, most of the important RIFFLE variables were noninsects and Diptera. For the 55-taxa density data (Table 5), the most important taxa were Chironomidae (Diptera), *Lymanea* (Mollusca), *Gyraulus* (Mollusca), *Anodonta* (Mollusca), Oligochaeta, *Dugesia tigrina* (Platyhelminthes), *Daphnia magna* (Crustacea), and *Hyalella azteca* (Crustacea). When the 55 taxa were condensed into 11 categories, the most important taxa were Diptera, Mollusca, Platyhelminthes, and Crustacea. Similar results were obtained for both 55 taxa and 11-category biomass data.

Discussion

In answer to our initial hypothesis, we found that there were significant differences in the Cannery Pond macroinvertebrate assemblages on different macrophyte species, and that these differences were most strongly related to whether the plant

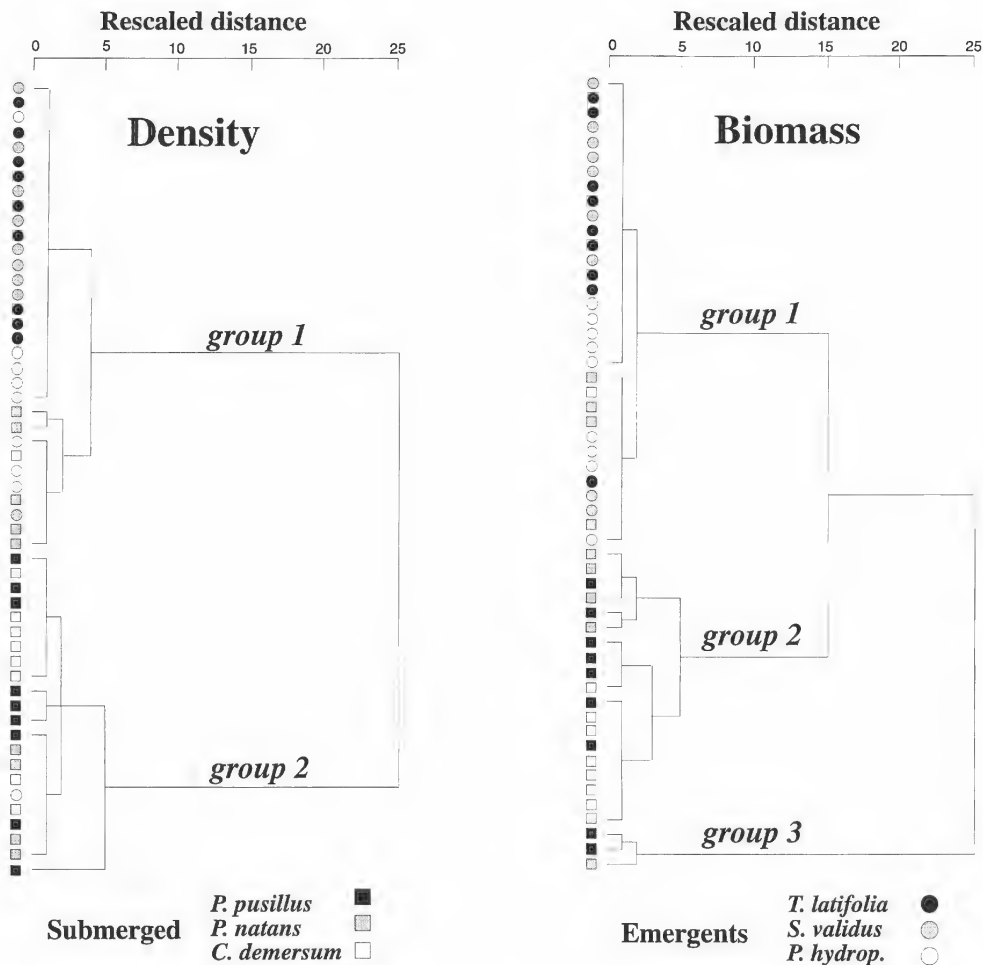


Figure 1. Cluster diagram of July and August macrophyte samples ($n=56$) based on macroinvertebrate density (#/kg plant wet wt) and biomass (mg/kg plant wet wt). Clustering procedure used Ward's method (minimum variance clustering) with squared Euclidean distance for 11 macroinvertebrate subcategories.

was submerged or emergent. The submerged plants, which generally supported the greatest density and biomass of macroinvertebrates, all had finely divided or thin submerged leaves and large surface areas per unit weight, suggesting that these morphological properties create a favorable habitat for many aquatic macroinvertebrates. The nature of the colonizable surface appeared to be at least as important as total surface area. The soft stemmed *P. natans* and *P. pusillus* contained more macroinvertebrates than did *C. demersum*, which

has brittle leaves that are tightly packed into whorls. Aquatic macrophytes are not just passive substrates for periphyton attachment (Blindow 1987). Many factors, including macrophyte species, plant age, and depth in the water column can affect the density of epiphytes, which in turn can determine the quality of the macrophyte as a substrate for macroinvertebrates. Although periphyton was not measured, it is possible that the epiphytes on the *Potamogeton* species provided a better food source

TABLE 5. RIFFLE cluster assignments based on macroinvertebrate densities for 55 taxa*. Similar numbers indicate samples that were assigned to the same RIFFLE cluster.

	Cluster assignment into 6 groups by sample date (rep=3, PRE=0.49, $\chi^2=0.99$)**								
	14-Jul	14-Jul	14-Jul	3-Aug	3-Aug	3-Aug	24-Aug	24-Aug	24-Aug
<i>S. tabernaemontani</i>	6	1	1	1	1	4	3	1	6
<i>T. latifolia</i>	1	6	6	3	3	6	6	6	3
<i>P. hydrop.</i>	5	6	6	4	3	5	3	4	5
<i>P. natans</i>	3	5	5	4	4	3	2	2	2
<i>C. demersum</i>	4	4	2	5	4	3	2	3	5
<i>P. pusillus</i>	2	4	2	6	4	2	5	2	2

	Cluster assignment into 6 groups by sample date (rep=3, PRE=0.49, $\chi^2=0.99$)**								
	14-Jul	14-Jul	14-Jul	3-Aug	3-Aug	3-Aug	24-Aug	24-Aug	24-Aug
<i>S. tabernaemontani</i>	1	1	1	1	1	2	1	1	1
<i>T. latifolia</i>	1	1	1	1	1	1	1	1	1
<i>P. hydrop.</i>	1	1	1	2	1	2	1	1	1
<i>P. natans</i>	2	2	2	1	1	2	2	2	2
<i>C. demersum</i>	2	1	2	2	2	2	2	2	2
<i>P. pusillus</i>	2	2	2	2	2	2	2	2	2

*These results do not include the September samples.

**PRE is the RIFFLE proportional reduction in error term, and χ^2 is the significance of the association between RIFFLE cluster and plant group.

for grazing macroinvertebrates than the other plant taxa.

The number of taxa found on each plant species ranged from 29 on *P. pusillus* to 42 on *T. latifolia*. *Potamogeton pusillus*, which had the greatest density and biomass of macroinvertebrates, had the lowest number of taxa (although this may not hold true if all taxa were identified to the same taxonomic level). Conversely, *T. latifolia*, with 42 taxa, consistently had low macroinvertebrate densities and biomasses. Although *P. pusillus* was not collected in September, it is unlikely that this alone accounted for the differences in number of taxa because the macroinvertebrate taxonomic richness on the other macrophytes was low during the fall (Parsons 1992). It is possible that the differences were due to seasonal differences in available habitat for the macroinvertebrates. The *T. latifolia* in Cannery Pond have finely-divided, persistent, suspended root mats that could provide macroinvertebrate habitat throughout the year, whereas the *P. pusillus* senesces in early fall, and could not provide winter or early spring habitat.

The most abundant insects on the submerged plants were Chironomids (Diptera). Chironomidae occupy many trophic levels; some feed mainly on periphyton, some mine macrophyte vegetation (Soszka 1975, Dvorak and Best 1982), and others are predaceous (Merritt and Cummins 1984). Submerged vegetation typically has extensive periphytic growth, relatively soft leaves for mining, an abundance of other macroinvertebrates that could serve as prey, and structural complexity that provides shelter from predators. These characteristics would satisfy many chironomid habitat requirements.

Among the noninsects, the crustacean amphipod *Hyalella azteca*, which feeds on Aufwuchs (Pennak 1978), was very numerous on the submerged vegetation. Similar results were reported by Voigts (1976), Schramm et al. (1987), and Chilton (1990) who found amphipods to be very abundant on submerged vegetation with finely divided leaves. Molluscs (especially *Lymnaea*, *Gyraulus*, and *Anodonta*) and annelids also were more common on the submerged plants in Cannery

Pond. Lodge (1985) also found *Lymnaea* to be abundant on submerged macrophytes. However, Voights (1976) and Hargeby (1990) found that animals that are slow to colonize areas of new macrophyte growth, such as molluscs, were less common on plants that die back during winter. These conflicting results were apparently due to differences in the availability of winter habitat (Voights' and Hargeby's studies were conducted in Iowa and southern Sweden, respectively; areas with severe winters). Cannery Pond has a mild maritime climate and freezes infrequently. Although the submerged macrophytes die back in winter, the effect may not be so severe as to limit molluscan recolonization in spring. Oligochaetes, which accounted for most of the differences in annelid numbers and biomass, were particularly abundant on *P. pusillus* and *C. demersum*. In addition, the *Helobdella* leeches were most abundant on the floating-leaved pondweed *P. natans*. These leeches prefer vegetation in quiet water and a good gripping surface (Pennak 1978), both of which are provided by *P. natans*.

Although many of the macroinvertebrate taxa were more abundant on submerged plants, several taxa were associated with emergent plants, including the isopod *Asellus*, Ephemeroptera, and some of the Odonata (especially the heavy-bodied dragonfly *Anax*). These findings are consistent with the results reported by Voights (1976) and Rabe and Gibson (1984). Copepods also were found most frequently associated with the emergent plants, which in Cannery Pond provided greater access to open water than the submerged plants. This was substantiated by Voights (1976), who found copepods more frequently in open water than densely vegetated areas. Unlike other molluscs, limpets (Ancylidae) were most common on *T. latifolia* and the floating-leaved *P. natans*; these plants provide the broad, smooth surface required by the organisms. Two taxa known to be herbivorous on aquatic plants were collected: *Acentria* (Lepidoptera) and *Limnephilus* (Trichoptera) (Soszka 1975). They were found almost exclusively on *P. hydropiperoides*, which in Cannery Pond grew 0.5 m deep with both emergent and submerged leaves. Perhaps this indicated a food preference for this plant, although Soszka (1975) found these genera associated with *Potamogeton* species. Clearly there is a need for additional work on host specificity among herbivorous aquatic insects.

The multivariate results favored a two-group macrophyte classification (emergent or submerged) rather than six. While this seems intuitive for the two soft-stemmed, submerged species of *Potamogeton* and the visibly similar emergents, *T. latifolia* and *S. tabernaemontani*, it was surprising that *C. demersum* and *P. hydropiperoides* were not placed in separate groups. Both had morphological characteristics that distinguished them from the other plant species (*C. demersum* has tightly packed, finely divided leaf whorls, and *P. hydropiperoides* has stiff, submerged leaves similar to its emergent leaves). Both typically had lower macroinvertebrate densities than the other emergent and submerged plant taxa. However, multivariate analyses can find patterns that are consistent across many variables, even if the variables do not show obvious patterns when viewed independently. Although *C. demersum* typically had lower abundances of the dominant macroinvertebrates found on *Potamogeton* species, its entire macroinvertebrate assemblage was more similar to the submerged plants than to any of the emergent taxa. The same argument can be applied to *P. hydropiperoides* and its similarity to the other emergent plant species.

The two-group classifications probably occurred because the multivariate results were influenced by "common" (i.e., consistently having a large biomass or numerical abundance) macroinvertebrate taxa. Most of the cluster or group separations were based on differences in Crustacea, Mollusca, Annelida, and Diptera, and these differences were greater when the data were grouped by submerged or emergent category, rather than by individual plant taxa. It is not unusual for variance-derived statistics such as MANOVA and hierarchical clustering to be greatly affected by differences in variables that have a large number of observations (such as common macroinvertebrate taxa). Nonmetric clustering, however, does not use variance or distance measures to separate groups. Thus, one of its distinctions is its ability to identify both common and uncommon taxa (or other variables) that are strongly associated with groups. In the Cannery Pond data, the taxa that RIFFLE identified as important were all common, and thus the RIFFLE results were basically the same as the parametric results.

It appears that in Cannery Pond, most of the macroinvertebrates are habitat generalists that are

found in greater abundances on the submerged plants than on emergents. These results are consistent with what is known about macroinvertebrate-plant relationships on land. Although many terrestrial macroinvertebrates are host-specific, having evolved to overcome habitat and nutritional obstacles that are unique for each plant species, terrestrial phytophages usually exploit a variety of host plants so that most plants have a number of macroinvertebrate consumers (Strong et al. 1984).

The plant features that appeared to have had the greatest influence on macroinvertebrate associations in Cannery Pond were: 1) the macrophyte surface area, which was greatest for the submerged species and *P. hydrotipperoides*; 2) the nature of the available surface area, which was greater for the *Potamogeton* species than for *P. hydrotipperoides* and *C. demersum*; 3) the structural stability of *T. latifolia* and *S. tabernaemontani* that provided support for large crawling macroinvertebrates such as *Anax*; and 4) the persistence

of the suspended *T. latifolia* root mass, which may have helped increase the taxonomic richness by providing a year-round habitat. A few unique macroinvertebrate-macrophyte associations also were discovered. Although these unique associations were not the dominant pattern in the data, they should be investigated further to see if they can be explained on the basis of specific habitat requirements for those macroinvertebrate taxa.

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Literature Cited

- APHA. 1989. Standard Methods for Examination of Water and Wastewater, 17th ed. American Public Health Association, American Water Works Association, Water Pollution Control Federation, Washington, D.C.
- Biochino, A. A. and G. I. Biochino. 1979. Quantitative estimation of phytophilous invertebrates. *Hydrobiological Journal* 15:74-76.
- Blindow, I. 1987. The composition and density of epiphyton on several species of submerged macrophytes - the neutral substrate hypothesis tested. *Aquatic Botany* 29:156-168.
- Brown, C. L., T. P. Poe, J. R. P. French and D. W. Schloesser. 1988. Relationships of phytomacrofauna to surface area in naturally occurring macrophyte stands. *Journal of the North American Benthological Society* 17:129-139.
- Chilton, E. W. II. 1990. Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria spiralis*) in Lake Onalaska, Wisconsin. *Journal of Freshwater Ecology* 5:444-466.
- Downing, J. A. 1986. A regression technique for the estimation of epiphytic invertebrate populations. *Freshwater Biology* 16:161-173.
- Dvorac, J. and E. P. H. Best. 1982. Macroinvertebrate communities associated with the macrophytes of Lake Vetchen: structural and functional relationships. *Hydrobiologia* 95:115-126.
- Findlay, S., K. Schoeberl and B. Wagner. 1989. Abundance composition and dynamics of the invertebrate fauna of a tidal freshwater wetland. *Journal of the North American Benthological Society* 8:140-148.
- Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65:455-468.
- Hargeby, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos* 57:338-346.
- Lodge, D. M. 1985. Macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. *Freshwater Biology* 15:695-708.
- Matthews, G. B. and J. W. Hearne. 1991. Clustering without a metric. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 13:175-184.
- Matthews, G. B., R. A. Matthews and W. G. Landis. 1995. Nonmetric conceptual clustering in ecology and ecotoxicology. *AI Applications* 9:41-48.
- Merritt, R. W. and K. W. Cummins. 1984. *An Introduction to the Aquatic Insects of North America*, 2nd ed. Kendall Hunt Publishing Co., Iowa.
- Minshall, G. W. 1984. Aquatic insect-stratigraphic relationships. In V. H. Resh and D. M. Rosenberg (eds.) *The Ecology of Aquatic Insects*, Praeger Publishers, New York, NY.
- Murkin, H. R. and D. B. J. Batt. 1987. Interactions of vertebrates and invertebrates in peatlands and marshes. In D. M. Rosenberg and G. V. Danks (eds.) *Aquatic Insects of Peatlands and Marshes in Canada*, Memoirs Entomological Society of Canada.
- Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* 10:89-114.
- Parsons, J. K. 1992. An evaluation of associations between macroinvertebrates and macrophytes in Cannery Pond, Washington. M.S. thesis, Western Washington University, Bellingham, WA.

- Rabe, F. W. and F. Gibson. 1984. The effect of macrophyte removal on the distribution of selected invertebrates in a littoral environment. *Journal of Freshwater Ecology* 2:359-371.
- Reger, S. J., C. F. Brothersen, T. G. Osborn and W. T. Helm. 1982. Rapid and effective processing of macroinvertebrate samples. *Journal of Freshwater Ecology* 1:451-465.
- Schramm, H. L., K. J. Jirka and M. V. Hoyer. 1987. Epiphytic macroinvertebrates in dominant macrophytes in two central Florida lakes. *Journal of Freshwater Ecology* 4:151-161.
- Soszka, G. J. 1975. Ecological relations between invertebrates and submerged macrophytes in the lake littoral. *Ekologia Polska* 3:393-415.
- SPSS, Inc. 1988. *SPSS-X User's Guide*, 3rd ed. SPSS Inc., Chicago, IL.
- Strong, D. R., J. H. Lawton and R. Southwood. 1984. *Insects on Plants, Community Patterns and Mechanisms*. Harvard University Press, Cambridge, MA.
- Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. In V. H. Resh and D. M. Rosenberg (eds.) *The Ecology of Aquatic Insects*, Praeger Publishers, New York, NY.
- Voigts, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. *American Midland Naturalist* 95:313-322.
- Wrubleski, D. A. 1987. Chironomidae of Peatlands and Marshes in Canada. In D. M. Rosenberg and H. V. Danks (eds.) *Aquatic Insects of Peatlands and Marshes in Canada*, *Memoirs Entomological Society of Canada*.

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Tree Wound Dynamics in Thinned and Unthinned Stands of Grand Fir, Ponderosa Pine, and Lodgepole Pine in Eastern Oregon

Abstract

The effects of thinning (spacing) on stem-wound closure and associated wood decay, as affected by tree growth and vigor, were tested in stands of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and lodgepole pine (*P. contorta* var. *latifolia* Engelm.). In stands located near Union, Cove, and Lapine, Oregon, thinning improved diameter growth and vigor. Vigor was indicated by measuring cambial electrical resistance. Wounds on trees in thinned stands tended to close faster than wounds on trees in unthinned stands, although differences were significant for lodgepole pine only. Stem decay occurred only in grand fir, and most of the decay was caused by *Heterobasidion annosum* (Fr.) Bref. The percentage of stem decay was significantly less in thinned (38.2%) than in unthinned (52.3%) firs. Our results support the use of thinning to improve pine and fir growth and reduce losses from wound-associated stem decay.

Introduction

Tree wounding often leads to stem decay in western conifers (Etheridge and Craig 1976, Aho 1977, Goheen et al. 1980, Aho and Filip 1982, Hinds et al. 1983, Filip et al. 1992). Wounds can either activate dormant decay fungi (hymenomycetes) or act as entry courts for fungal spores. The decay process in living trees may depend on tree species, vigor, and wound frequency, size, and severity.

Tree vigor is both difficult to define and measure. Shigo (1985) defines vigor as "the genetically controlled capacity—potential—to survive after injury or infection." Wargo and Skutt (1975) suggest that measuring electrical properties of trees may be a method for determining tree vigor and further suggest using cambial electrical resistance (CER) as an indicator of tree vigor. Resistance to a pulsed-electric current delivered to the cambium indicates relative changes in concentrations of mobile cations, especially potassium, and is inversely proportional to ion concentration. As suggested by Shortle et al. (1977), vigorous trees have a lower CER than do less vigorous trees. Measuring CER with an instrument known as a Shigometer is relatively easy and fast in the field.

CER has been compared to other methods for determining tree vigor such as measuring the ratio of current basal area growth to sapwood area as an estimator of stemwood-volume production per unit of leaf area (Waring et al. 1980). Tree

vigor, as indicated by basal area growth/sapwood area showed good correlations with vigor as indicated by CER for grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) ($r^2=0.67$, $n=30$) (Filip et al. 1989) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) ($r^2=0.41$, $n=80$) (Filip, unpublished).

In the northeastern United States, CER measurements indicate that hardwoods in stands that have been thinned (spaced) for three years are more vigorous than are those in unthinned stands (Smith et al. 1976). Trees with increased vigor in thinned stands, therefore, may react differently to wounding than do trees in unthinned stands. In addition, wound closure occurs faster in northeastern hardwoods that are more vigorous (Neely 1983) and have lower CER values (Shortle et al. 1977, Wargo 1977). In grand fir stands in southern Oregon, artificially inflicted wounds tended to close more rapidly on trees in thinned stands than on trees in unthinned stands, but differences were not significant (Filip et al. 1992).

Although wound closure may be directly related to tree vigor, the amount of internal discoloration and decay associated with a wound may be independent of tree vigor; such is the case for hybrid poplars (Shortle et al. 1977) and possibly other tree species (Shigo 1986). In Oregon and Washington, the proportion of decay in western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Goheen et al. 1980) was less in thinned stands, because trees in stands thinned several years previously were larger and had compensated for decay by

increased growth. Thus, western conifers that have been thinned and are growing more rapidly appear to develop a smaller percentage of decay than do trees in unthinned stands. Grand fir is considered very susceptible to stem decay in Oregon (Aho 1977, Aho et al. 1987). Lodgepole pine and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) are considered relatively resistant to decay, however, little research concerning decay in these species has been done in Oregon.

Objectives of our study were to determine the effects of thinning on 1) the rate of wound closure, and 2) the amount of wound-associated decay, as influenced by tree growth and vigor.

Three tree species were chosen for study: grand fir, ponderosa pine, and lodgepole pine.

Methods

Study Site and Stand Characteristics

The grand fir study site is a grand fir/queen's cup (*A. grandis*/*Clintonia uniflora*) plant association (Johnson and Simon 1987) and is about 7 km SE of Cove, Oregon in the Wallowa-Whitman National Forest. Elevation is 1675 m, with a 40% slope and NW aspect. Site index is 16.1 m at 50 yrs (Cochran 1979); this is a conservative estimate, because the stand had been defoliated by the western spruce budworm (*Choristoneura occidentalis* Freeman) since 1981. The stand is composed primarily of grand fir with some Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), western larch (*Larix occidentalis* Nutt.), and lodgepole pine. Part of the stand was precommercially thinned in 1973. Although initial spacing guidelines and resulting residual basal areas are not known, basal area (m^2/ha) surrounding each sample tree in 1986 averaged 10.7 and 34.8 for thinned and unthinned parts of the stand. When sampled in 1989, the stand was 65 yrs old with a mean diameter breast height (DBH), 1.4 m above ground, of 19 cm. The thinning stumps were infected with *Armillaria* sp. (North American Biological Species 10) and *Heterobasidion annosum*.

The ponderosa pine study site is a grand fir/pine grass (*Abies grandis*/*Calamagrostis rubescens*) plant association (Johnson and Simon 1987) and is about 25 km SE of Union, Oregon in the Wallowa-Whitman National Forest. Eleva-

tion is 1200 m, with a 5% slope and NW aspect. Site index is 38.7 m at 100 yrs (Barrett 1978). The stand is composed primarily of ponderosa pine with some Douglas-fir and grand fir. Part of the stand was precommercially thinned in 1973. Although initial spacing guidelines and resulting residual basal areas are not known, basal area (m^2/ha) in 1986 averaged 19.1 and 23.0 for thinned and unthinned parts of the stand. When sampled in 1989, the stand was 32 yrs old and average DBH was 21 cm.

The lodgepole pine study site is a lodgepole pine/bitterbrush/needlegrass (*Pinus contorta*/*Purshia tridentata*/*Stipa occidentalis*) plant association (Volland 1976) and is about 25 km E of Lapine, Oregon in the Deschutes National Forest. Elevation is 1675 m, and the topography is flat. Site index is 12.4 m at 50 yrs (Dahms 1964). The stand is composed entirely of lodgepole pine. Part of the stand was precommercially thinned in 1980 to three target spacings: 4.3, 5.6, and 6.9 m (Mitchell and Preisler 1991). These spacings correspond to 1986 basal areas surrounding each sample tree of 10.6, 6.5, and 5.3 m^2/ha , respectively. Basal areas surrounding each sample tree in unthinned parts of the stand averaged 23.7 m^2/ha . When sampled in 1989, the stand was 125 yrs old and average DBH was 22 cm. As described by Mitchell and Preisler (1991), mortality was occurring from infestation by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and some trees were infected by dwarf mistletoe (*Arceuthobium americanum* Nutt.).

Tree Selection, Wounding, and Monitoring

Within each stand, trees were randomly selected within a specified DBH range (15 to 22 cm) to minimize initial differences in diameter and CER. Each selected tree was marked with a numbered metal tag at 0.3 m above ground. In June 1986, 20 trees were artificially wounded and another 20 trees left unwounded within both thinned and unthinned portions of each stand. Thus, a total of 80 trees (40 in thinned and 40 in unthinned) of each species were treated. In the lodgepole pine stand, 10 trees were wounded and 10 trees left unwounded in each of the four treatments (60 in thinned and 20 in unthinned). Only trees that were unwounded and non-decayed at 1.4 m above ground (as detected by increment boring completely through the stem) were selected for wounding.

Trees were artificially wounded as follows: each tree received two circular wounds, 25 mm in diameter and 50 mm deep from cambium to pith at breast height on N and S sides of the tree (Figures 1 and 2). Wounds were drilled with a hand auger and bit and were centered directly over the hole made by the increment borer that tested for decay. Three years after wounding, the final wound diameter was calculated by averaging measurements (with a caliper) of the diameter (nearest 0.1 mm) of the opening of both wounds on each tree. For both wounded and unwounded trees, DBH (nearest mm) was measured with a diameter tape at the wound center in June 1986 and October 1989 (after four growing seasons). These years were generally drier than normal for eastern Oregon.



Figure 1. Artificial wounding of a ponderosa pine with a hand auger and bit.

In June 1989, 3 yrs after wounding, CER was determined with a Shigometer Model OZ-67. Needle probes were pushed vertically through the bark into the wood. For each tree, the average of CER measurements (nearest K ohm) at four points around each stem at 1.4 m above ground was calculated. All CER measurements were taken during the active growing season (June) on consecu-

tive days at about the same time each day to minimize variation resulting from temperature and weather conditions.

Stem Decay

In October 1989, all wounded trees were felled, and 45-cm long stem sections above the top of the wounds were tagged and transported to the laboratory. Sections were refrigerated at 2°C until they were processed within 1 wk of sampling. Ten unwounded trees were also felled in each stand to determine whether or not decay was present.

In the laboratory, the cross-sectional area (nearest cm²) of decay on the wounded end of each segment was estimated as follows: incipient and advanced decay in the cross-section was outlined with pen. The area of the outlined portion (decay area) was estimated with a clear plastic sheet containing a grid of 1-cm² squares that fell within the outlined portion. Wetwood was distinguished visually from incipient decay. The percentage of decay was then calculated by dividing the decay area by the total cross-sectional area of the stem segment and multiplying by 100.

The frequencies of hymenomycetes and associated microorganisms were determined by aseptically splitting each stem segment through the two wounds (Figure 2). Ten wood chips (5 x 5 x 10 mm) were removed at 2-cm intervals above each wound at a depth of 2 cm beyond the cambium. Isolations were attempted from clear wood, wetwood, incipient decay, and advanced decay. Each wood chip was placed in a tube containing 2% malt agar and incubated for 6 wks at room temperature in the dark. All hymenomycetes were identified to species, if possible, by culture morphology and chemical tests by the Center for Mycology Research, Madison, WI. The isolation frequencies of bacteria/yeasts, nonhymenomycetes, and hymenomycetes were recorded.

Statistical Analysis

Data were analyzed by the General Linear Models Procedure of the SAS/STAT Package Version 6 (SAS Institute, Inc. 1987). Significant differences ($p \leq 0.05$) between thinned and unthinned portions of each stand were determined by two-way analysis of variance for 1) vigor (as indicated by CER) of wounded and unwounded trees, and 2) DBH growth of wounded and unwounded trees, and by one-way analysis of variance for

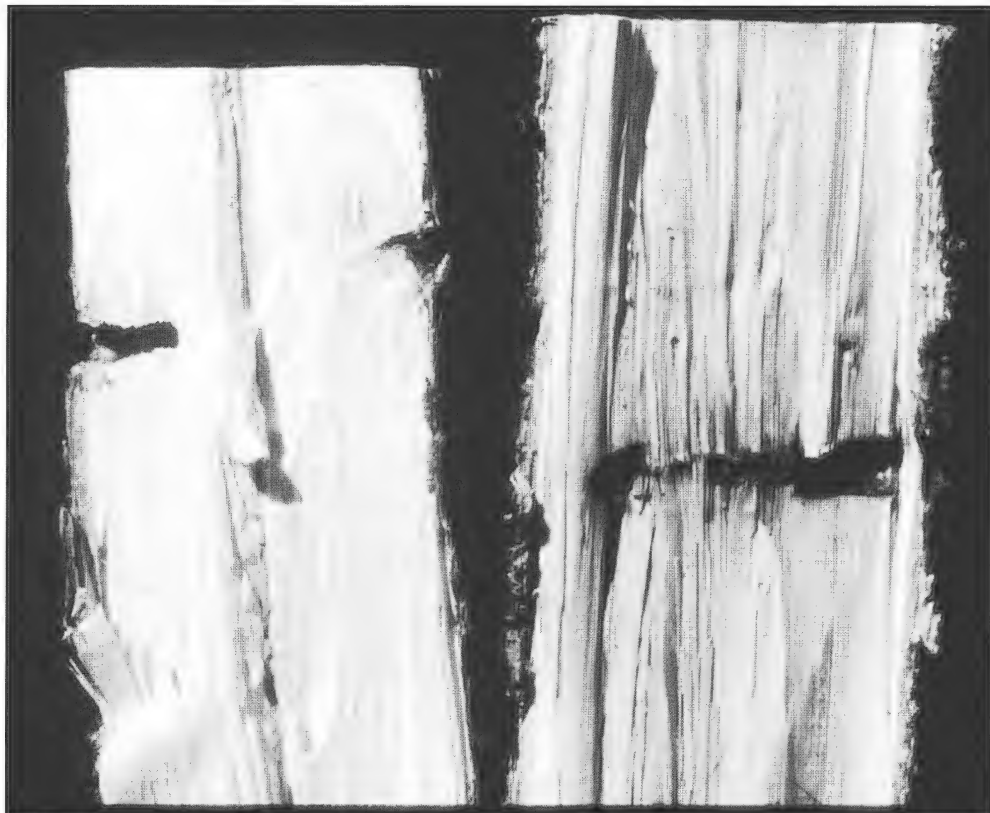


Figure 2. Typical decay (darker-colored wood) caused primarily by *Heterobasidion annosum* in a grand fir stem (right) 3 yrs after infliction of two wounds (2.5 x 5.0 cm) on opposite sides of the tree. There was no decay in similarly treated ponderosa pine (left) or lodgepole pine. The diameter of the drill holes in each stem section is 2.5 cm.

1) final wound diameter, 2) decay area, and 3) percentage decay. For the lodgepole pine stand, significant differences among the four spacings were determined by Fisher's Least Significant Difference test.

Results

Grand Fir Stand

Thinning significantly improved tree vigor, as indicated by CER, and increased tree diameter growth (Tables 1 and 2). Also, wounded trees were significantly more vigorous (lower CER) and had greater DBH growth than unwounded trees. Final wound diameters tended to be smaller for trees in thinned portions, but these differences were not significant. Average wound diameters per tree

ranged from 6.7 to 18.9 mm. Wound diameters on the same tree ranged from 7.5 to 17.1 mm. Although trees in thinned areas tended to have less total decay area, differences were significant only for percentage of decay. All of the wounded trees had either incipient or advanced decay (Table 3), but no decay was found in any of the unwounded trees sampled. Most of the decay was caused by *Heterobasidion annosum*, which also comprised over half of the total isolation attempts on agar media. No differences in the type or number of microorganisms were apparent between trees in thinned and unthinned portions of the stand.

Ponderosa Pine Stand

Tree vigor as indicated by CER was significantly greater for trees in thinned areas (Table 1). No

TABLE 1. Tree and wound characteristics in thinned and unthinned portions of grand fir, ponderosa pine, and lodgepole pine stands in eastern Oregon.

	Grand fir		Ponderosa pine		Lodgepole pine			
					Thinned, by spacing			
	Unthinned	Thinned	Unthinned	Thinned	Unthinned	4.3m	5.6m	6.9m
CER (K ohms)¹								
Unwounded	16.1	12.8	19.2	14.1	16.3	10.8	11.8	9.2
Wounded	12.8	10.5	15.5	13.3	14.9	9.6	11.1	9.2
Tree diameter growth (mm/yr)								
Unwounded	0.8	1.1	3.2	3.0	1.5	3.8	3.3	3.3
Wounded	2.1	3.6	6.4	7.9	1.5	4.8	3.6	5.5
Final wound diameter (mm)	14.4	12.5	13.4	11.0	21.2	16.1	17.1	14.2
Decay area (cm²)	111.6	92.2	0	0	0	0	0	0
Decay area (%)	52.3	38.2	0	0	0	0	0	0

¹ Low values (CER) indicate high vigor; high values indicate low vigor.

TABLE 2. Analysis of variance for the treatments thinning, wounding, and interactions in grand fir, ponderosa pine, and lodgepole pine stands in eastern Oregon.

Treatment	Grand fir				Ponderosa pine				Lodgepole pine			
	DF ¹	MS	F	Pr>F	DF	MS	F	Pr>F	DF	MS	F	Pr>F
CER												
Thinning	1	147	14.6	0.0003	1	267	7.3	0.0086	3	153	11.0	0.0001
Wounding	1	155	15.4	0.0002	1	106	2.9	0.0923	1	14	1.0	0.3213
Interaction	1	6	0.6	0.4371	1	33	0.9	0.3455	3	2	0.1	0.9394
Error	74	10			70	36			69	14		
Tree diameter growth												
Thinning	1	1	4.6	0.0346	1	3	0.5	0.4773	3	38	9.3	0.0001
Wounding	1	9	45.4	0.0001	1	265	51.7	0.0001	1	17	4.3	0.0424
Interaction	1	0.2	0.8	0.3682	1	6	1.1	0.3031	3	5	1.2	0.3354
Error	74	0.2			74	5			72	4		
Final wound diameter												
Thinning	1	31	3.8	0.0594	1	58	2.8	0.1007	3	88	15.4	0.0001
Error	38	8			38	21		34	6			
Decay area												
Thinning	1	3783	1.5	0.2262		—	—	—		—	—	—
Error	38	2500				—		—				
Percent decay												
Thinning	1	2002	4.1	0.0489		—	—	—		—	—	—
Error	38	484				—		—				

¹DF = Degrees of freedom; MS = Mean square; F = F-value; and Pr>F = Probability greater than F-value.

TABLE 3. Frequency of *Heterobasidion annosum*, non-decay fungi, and bacteria/yeasts isolated from artificially wounded grand fir, ponderosa pine, and lodgepole pine in thinned and unthinned portions of the stands.

	Grand fir		Ponderosa pine		Lodgepole pine	
	Thinned	Unthinned	Thinned	Unthinned	Thinned	Unthinned
Trees (no.)	20	20	20	20	30	10
Trees with decay (no.)	20	20	0	0	0	0
Trees with <i>H. annosum</i> (no.)	15	16	0	0	0	0
Isolations (no.)	200	200	200	200	300	100
No growth (%)	8	30	12	15	21	11
Bacteria/yeasts (%)	3	2	1	0	0	1
Non—decay fungi (%)	31	19	87	85	79	88
<i>H. annosum</i> (%)	58	49	0	0	0	0

significant difference in diameter growth existed between trees in thinned and unthinned portions, but neither were there significant differences in basal area between thinned and unthinned parts of the stand. Wounded trees tended to be more vigorous but not significantly, and had significantly increased diameter growth. Final wound diameters tended to be smaller for trees in thinned areas, but these differences were not significant. Average wound diameters per tree ranged from 2.5 to 21.6 mm. Wound diameters on the same tree ranged from 0 (completely closed) to 14.4 mm. No decay was found in any of the wounded or unwounded ponderosa pine trees, and no hymenomycetes were isolated 3 yrs after wounding (Table 3).

Lodgepole Pine Stand

Tree vigor (as indicated by CER) and diameter growth were significantly higher in thinned areas; there were no significant differences among spacings (Tables 1 and 2). Wounded trees tended to be more vigorous and had more DBH growth than unwounded trees, however, differences were significant for diameter growth only. Final wound diameters were significantly smaller for trees in thinned portions and significantly smallest at the widest tree spacing. Average wound diameters per tree ranged from 7.3 to 20.2 mm. Wound diameters on the same tree ranged from 9.5 to 21.0 mm. As with ponderosa pine, no decay occurred in any of the wounded or unwounded lodgepole pine trees, and no hymenomycetes were isolated 3 yrs after wounding (Table 3).

Discussion

Thinning tended to maintain increased tree vigor and diameter growth several years after treatment

for stands of grand fir (after 16 yrs), ponderosa pine (after 16 yrs), and lodgepole pine (after 10 yrs). These findings are similar to results reported for vigor in northeastern hardwoods (Smith et al. 1976). Wounded trees in our study tended to be more vigorous (lower CER) and show more diameter growth than did unwounded trees. We speculate that, because both vigor (CER) and growth were measured at the wound site for all species, the formation of new callous tissue in response to wounding may have stimulated diameter growth and vigor in that portion of the stem. Wound closure was always from the sides of the wound and tended to be faster in thinned portions of grand fir, ponderosa pine, or lodgepole pine stands. These trees were faster growing than those in unthinned portions. Although wound closure tended to be faster in trees in thinned portions of all stands, differences were statistically significant for the lodgepole pine stand only. This lack of significance may be the result of variation in wound closure rates among trees and even between the two wounds on the same tree. We reported similar results for grand fir in southern Oregon (Filip et al. 1992).

The amount of stem decay in grand fir appears to be independent of wound closure, an observation also reported for hybrid poplars (Shortle et al. 1977) and other hardwoods (Shigo 1986). However, the percentage of stem decay in grand fir was less in trees in thinned portions. This is probably a result of increased tree radial growth that compensates for the loss from decay. Comparable results have been observed in wounded grand fir stands in northeastern Oregon (Aho 1977) and southern Oregon (Filip et al. 1992), and in thinned western hemlock stands in western Or-

egon and Washington (Goheen et al. 1980). In all four studies, stem decay was confined to the cylinder of wood present at the time of wounding (Figure 2), a process known as compartmentalization (Shigo 1984). Hence, after 3 yrs, the faster growing trees had added more clear wood to the decayed cylinder than had the slower growing trees. These differences would have been more dramatic had more years been allowed for growth.

Three years after traumatic wounding, stem decay was not present in ponderosa or lodgepole pine, but was extensive in grand fir. Stem decay in grand fir was also extensive in a similar study in southern Oregon (Filip et al. 1992). Most of the decay in both studies was caused by *Heterobasidion annosum*, which is a common root, butt, and stem decay fungus. A 1979 survey of advance grand fir regeneration showed that *H. annosum* and *Echinodontium tinctorium* (Ell. & Ev.) Ell. & Ev. produced the most decay in 20 stands throughout Oregon and Washington (Aho et al. 1987).

In the present study, it was assumed that *H. annosum* entered all trees through airborne-spore infections of artificially created wounds rather than through roots, because all decay columns were confined to the immediate wound area and did not extend to the ground. *Heterobasidion annosum* can also enter living trees via root contacts with infected adjacent stumps. However, small-diameter stumps such as those created through precommercial thinning generally do not result

in infection of adjacent living pine or fir in the Pacific Northwest.

In conclusion, stem decay associated with wounding may be extensive after 3 yrs in grand fir, but initially not present in either ponderosa or lodgepole pine. However, although thinning may result in some wounding and subsequent stem decay in residual grand firs, the percentage of stem decay is likely to be lower in thinned stands than in unthinned stands. This finding is the result of increased diameter growth associated with thinning. In similar grand fir stands where wood production is to be maximized, we recommend precommercial thinning but suggest that wound prevention guidelines (Aho et al. 1983) be followed to further reduce damage and subsequent stem decay. Although no decay was found in wounded stands of ponderosa or lodgepole pine, we recommend thinning to increase growth and vigor and offset any decay that may develop after several years.

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Literature Cited

- Aho, P. E. 1977. Decay of grand fir in the Blue Mountains of Oregon and Washington. USDA For. Serv. Res. Pap. PNW-229. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 18 p.
- Aho, P. E., G. Fiddler, and G. M. Filip. 1983. How to reduce injuries to residual trees during stand management activities. USDA For. Serv. Gen. Tech. Rep. PNW-156. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 17 p.
- Aho, P. E., and G. M. Filip. 1982. Incidence of wounding and *Echinodontium tinctorium* infection in advanced white fir regeneration. Can. J. For. Res. 12:705-708.
- Aho, P. E., G. M. Filip, and F. F. Lombard. 1987. Decay fungi and wounding in advance grand and white fir regeneration. For. Sci. 33:347-355.
- Barrett, J. W. 1978. Height growth and site index curves for managed, even-aged stands of ponderosa pine in the Pacific Northwest. USDA For. Serv. Res. Pap. PNW-232. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 14 p.
- Cochran, P. H. 1979. Gross yields for even-aged stands of Douglas-fir and white or grand fir east of the Cascades in Oregon and Washington. USDA For. Serv. Res. Pap. PNW-263. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 17 p.
- Dahms, W. G. 1964. Gross and net yield tables for lodgepole pine. USDA For. Serv. Res. Pap. PNW-8. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 14 p.
- Etheridge, D. E., and H. M. Craig. 1976. Factors influencing infection and initiation of decay by the Indian paint fungus (*Echinodontium tinctorium*) in western hemlock. Can. J. For. Res. 6:299-318.
- Filip, G. M., E. Christiansen, and C. A. Parks. 1989. Secondary resin production increases with vigor of *Abies grandis* inoculated with *Trichosporium symbioticum* in northeastern Oregon. USDA For. Serv. Res. Note PNW-RN-489. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. 11 p.
- Filip, G. M., B. E. Wickman, R. R. Mason, C. A. Parks, and K. P. Hosman. 1992. Thinning and nitrogen fertilization in a grand fir stand infested with western spruce budworm. Part III: Tree wound dynamics. For. Sci. 38:265-274.

- Goheen, D. J., G. M. Filip, C. L. Schmitt, and T. F. Gregg. 1980. Losses from decay in 40- to 120-year old Oregon and Washington western hemlock stands. USDA For. Serv., R6-FPM-045-1980, Pac. Northw. Region, Portland, Oregon. 19 p.
- Hinds, T. E., R. E. Wood, and R. L. Bassett. 1983. Wounds and decay in residual corkbark fir. USDA For. Serv. Res. Pap. RM-247. Rocky Mtn. For. and Range Exp. Sta., Fort Collins, Colorado. 6 p.
- Johnson, C. G., Jr., and S. A. Simon. 1987. Plant associations of the Willowa-Snake Province. USDA For. Serv. R6-ECOL-TP-255A-86. Pac. Northw. Region, Portland, Oregon. 400 p.
- Mitchell, R. G., and H. K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *For. Sci.* 37:1390-1408.
- Neely, D. 1983. Tree trunk growth and wound closure. *Hortic. Sci.* 18:99-100.
- SAS Institute, Inc. 1987. SAS/STAT™ guide for personal computers. Version 6. Cary, NC. 1028 p.
- Shigo, A. L. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. *Ann. Rev. Phytopathol.* 22:189-214.
- _____. 1985. Wounded forests, starving trees. *J. of For.* 83:668-673.
- _____. 1986. A new tree biology: facts, photos, and philosophies on trees and their problems and proper care. Shigo and Trees, Assoc., Durham, New Hampshire. 595 p.
- Shortle, W. S., A. L. Shigo, P. Berry, and J. Abusamra. 1977. Electrical resistance in tree cambium zone: relationship to rates of growth and wound closure. *For. Sci.* 23:326-329.
- Smith, D. E., A. L. Shigo, L. O. Safford, and R. Blanchard. 1976. Resistances to a pulsed electrical current reveal differences between nonreleased, released, and released-fertilized paper birch trees. *For. Sci.* 22:471-472.
- Volland, L. A. 1976. Plant communities of the central Oregon pumice zone. USDA For. Serv. R-6 Area Guide 4-2. Pac. Northw. Region, Portland, Oregon. 113 p.
- Wargo, P. M. 1977. Wound closure in sugar maples: adverse effects of defoliation. *Can. J. For. Res.* 7:410-414.
- Wargo, P. M., and H. R. Skutt. 1975. Resistance to pulsed electric current: an indicator of stress in forest trees. *Can. J. For. Res.* 5:557-561.
- Waring, R. H., W. G. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. *For. Sci.* 26:112-117.

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Are Heart Rot Fungi Major Factors of Disturbance in Gap-Dynamic Forests?

Abstract

Heart rot fungi cause substantial economic loss in many forests, but their ecological roles in altering the speed or direction of succession are frequently overlooked. As heart rot induces trees to die standing or, more commonly, by bole breakage, the fungi that cause heart rot can be viewed as both pathogens and agents of disturbance. Many forests that do not experience frequent, large-scale disturbance, such as those where fire is rare, are composed of old trees. Heart rot fungi are abundant in these old forests and are important ecologically as disturbance agents by initiating and sustaining canopy gaps. Heart rot fungi also have profound influence on numerous structures and processes such as nutrient cycling, vegetation composition, and wildlife habitat. This paper uses the temperate rainforest of southeast Alaska to explore ecological consequences of heart rot, including the role of heart rot fungi in canopy gap formation. A thorough understanding of disturbance ecology in such forests must involve closely integrated research among ecologists, mycologists, and pathologists.

Introduction

Virtually every important timber species in North America is invaded and decayed by one or more species of heart rot fungi (Gilbertson and Ryvarden 1986). The same undoubtedly applies for other tree species throughout the world. A considerable body of literature on commercial loss by heart rot has been developed since Hartig (1874) described the causal relationship of fungi. But the ecological role of heart rot fungi as disturbance factors in forests has received very little attention. The purpose of this paper is to explore this concept.

I use the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)-Sitka spruce (*Picea sitchensis* (Bong.) Carr.) temperate rainforest of coastal Alaska to illustrate how heart rot fungi may influence disturbance ecology. These forests provide an excellent setting to explore the ecological function of such pathogens and the concept of forest health in an ecosystem because of the large forested areas present with little direct impact by humans. Vast forests still exist that have not been subjected to timber harvesting, forest management, or fire suppression. Other pathogens, such as hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) and fungi that cause root diseases, are not the major focus of this paper even though they cause some, but as yet unmeasured level of disturbance-mortality or alter stand structure or species composition in these forests.

Initial observation and knowledge of their intensive infection levels and more extensive distribution suggest that heart rots play more important ecological roles, particularly in causing disturbance. I hope that the ideas that follow, some of which are hypothetical and speculative, will stimulate thinking and encourage a better working relationship among ecologists, mycologists, and pathologists.

Forest Dynamics in Coastal Alaska

The forests of the southeast portion of coastal Alaska are composed by volume of approximately 61% western hemlock, 33% Sitka spruce, and 6% cedars and other species (Harris and Farr 1974). An estimated 31% of the overall gross volume of old-growth forests in southeast Alaska is defective (Farr et al. 1976). Several factors have probably contributed to such a high proportion of defect including hemlock and spruce's susceptibility to decay, their thin bark that is easily wounded, and a wet, mild climate favorable for the development and spread of fungi. Time may also be a critical factor. Many forests in coastal Alaska are composed of old trees because of the infrequency of large-scale catastrophic disturbance. Fires are uncommon and not considered an important disturbance factor in most areas (Harris and Farr 1974, Alaback 1988). Landslides, glacial rebound, and large-scale windthrow appear to be more common disturbances on sites where topography and

other factors are favorable for their occurrence (Ruth and Harris 1979). The more frequently disturbed sites host one of the several stand development phases leading to the true "old growth" stage as described by Oliver and Larson (1990). But on other sites, perhaps centuries or even millennia elapse between large-scale disturbance events. Without frequent disturbance, forests are allowed to reach and persist in the old-growth stage where fungi apparently have ample time to cause their slow, but persistent heart rot decay.

Succession in these old-growth forests appears to be occurring on many sites as the result of small-scale disturbance in the form of gap-phase development (Alaback 1988). Canopy gaps form when one or more trees die standing, when boles break (sometimes called windbreak or stem snap), when trees are uprooted (sometimes called windthrow), or combinations of these. The incidence of the various causes of tree mortality leading to gap formation is only now being measured. Preliminary results and observation in the region by ecologists and me suggest that all three types are common and bole breakage is often the leading cause of tree death. High winds, water-saturated soils, and shallow root systems lead to susceptibility for uprooting (Alaback 1988). Until now, the consequences of uprooting is the only effect of small-scale disturbance mortality that have received much study in these forests.

Heart rot fungi may also facilitate the change from the maturing even-aged stage (i.e., understory reinitiation, to use Oliver and Larson's (1990) terminology) that is in transition to the true old-growth stage. Mortality of dominant trees may be necessary for this transition or at least it speeds the rate of change. In the four forests in southeast Alaska at this stage of development (150 to 165 years old) in which I have made observations, each had substantial levels of heart rot and many large trees were dying as a result of bole breakage. By contrast, earlier stages (i.e., stand initiation and stem exclusion) of stand development lack both high levels of heart rot and bole breakage. Disease levels are generally low at these early stages; most trees die standing from factors associated with competition (Hennon et al. 1994).

Heart Rot Fungi in Coastal Alaska

The dominant species of heart rot fungi of western hemlock and Sitka spruce in coastal Alaska

(Table 1) are well known to mycologists and pathologists, all are found in conifers throughout the Pacific Northwest of North America. Brown and white rot species are well represented in both hosts. Western hemlock and Sitka spruce host a large number of fungi (Hepting 1971). These fungi have been shown by regional studies to vary widely in the amount of decay caused throughout the ranges of their hosts. For example, the fungus *Echinodontium tinctorum* (Ellis & Everh.) Ellis & Everh. is known to cause heavy losses in portions of the range of western hemlock (Foster et al. 1954) but is absent on this host in coastal Alaska.

TABLE 1. Decay fungi of living of Sitka spruce and western hemlock in forests of coastal Alaska listed in descending order of importance (modified from Kimmey (1956).

Sitka spruce
<u>White rot fungi</u>
<i>Phellinus pini</i> (Thore:Fr.) Pilat
<i>Armillaria</i> spp.
<i>Heterobasidion annosum</i> (Fr.) Bref.
<i>Merulius</i> sp.
<i>Phellinus nigrolimitatus</i> (Rom.) Bourd. & Galz.
<u>Brown rot fungi</u>
<i>Fomitopsis pinicola</i> (Schwartz:Fr.) Karst.
<i>Phaeolus schweinitzii</i> (Fr.) Pat.
<i>Laetiporus sulphureus</i> (Bull.:Fr.) Murr.
<i>Antrodia heteromorpha</i> (Fr.) Donk.
<i>Lentinus kaufmanii</i> A.H. Smith
Western hemlock
<u>White rot fungi</u>
<i>Armillaria</i> sp.
<i>Heterobasidion annosum</i>
<i>Pholiota adiposa</i> (Fr.) Kumm.
<i>Phellinus hartigii</i> (Allesch. & Schnabl) Bond.
<i>Phellinus pini</i>
<i>Ganoderma applanatum</i> (Pers.:Wallr.) Pat.
<u>Brown rot fungi</u>
<i>Fomitopsis pinicola</i>
<i>Laetiporus sulphureus</i>
<i>Phaeolus schweinitzii</i>
<i>Hericius</i> sp.

Heart rot fungi are specialized organisms that attack the heartwood of trees that are still living. They colonize and begin the decomposition process of wood before the tree is dead. Ecologically, some are pioneers of the wood substrate, the first organisms to inhabit wood. In other cases, a heart rot fungus, although causing the most destructive decay, may follow others in a succession of organisms colonizing the wood of living trees (Shigo 1967, Etheridge 1973).

These fungi have different degrees of specialization and modes of attack. Several species (e.g., *Fomitopsis pinicola* (Schwartz:Fr.) Karst. and *Laetiporus sulphureus* (Bull.:Fr.) Murr.) are common and ecologically important as brown rot decomposers of downed woody debris. These are opportunists, they spread by aerial dissemination of spores and, presumably, invade hemlock and spruce through wounds with exposed wood, first as a sap rot and then heart rot of live trees (Etheridge 1973). Other species (e.g., *Armillaria* spp. and *Phaeolus schweinitzii* (Fr.) Pat.) produce decay in roots and spread into the butt portion of trees' boles. These so called "butt rot fungi" are believed to initially enter trees through root infection (Kile et al. 1991). Some species (e.g., *Heterobasidion annosum* (Fr.) Bref.) are able to spread both by vegetative growth from the root system into the lower bole and by spores to invade wounds. All of these fungi are capable of continuing to decompose wood after their host tree has died, standing or down.

Several other heart rot fungi are restricted to causing decay only in living trees and have specialized modes of attack. Etheridge (1972) called these fungi the "true heart rots." The heart rot fungus *Echinodontium tinctorium* infects conifers through small twigs then remains dormant, perhaps for decades, until the tree is stressed or injured (Etheridge and Craig 1976). Large bole wounds are not infection courts for the true heart rot fungi but these injuries do stimulate their growth and decay activity. Several heart rot fungi do not confine their assault to heartwood inside the boles of live trees. Species such as *Phellinus hartigii* (Allesch. & Schnabl) Bond., *P. pini* (Thore:Fr.) Pilat, and *P. chrysoloma* (Fr.) Donk. (Owens 1936, Boyce and Wagg 1955) may grow into the sapwood and phloem, killing tissues as they advance. This type of attack can result in death of a side of the tree or of the entire tree.

The true heart rot fungus *P. pini* is a leading cause of heart rot in many living western conifers, including all species of spruce and hemlock in Alaska (Holsten et al. 1985). Its primary avenue for infecting heartwood is probably through dead branch stubs (Boyce 1961) or very small twigs (Haddow 1938). Boyce and Wagg (1955) suggest that this heart rot fungus has a cyclical pattern of infection throughout the developmental stages of old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. It infects vigorously growing Douglas-fir trees at about 50 years of age and, after most heartwood has been colonized, it attacks sapwood. Such trees experience a slowed radial growth and often die standing, sometimes 150-170 years after initial infection (Boyce and Wagg 1955). Because of its common occurrence (*P. pini* causes more than 80% of the heart rot in old-growth Douglas-fir) and through its habit of killing trees, this fungus may be a factor in the succession to shade-tolerant species such as western hemlock when stands reach 300-400 years of age.

What about heart rot in conifers with extremely decay resistant heartwood? Tree species in the Cupressaceae and Taxodiaceae, for example, have evolved to produce heartwood with high concentrations of compounds that retard the growth of decay fungi. Interestingly, each tree species has a complement of compounds which imparts its own unique aroma. These compounds have led to relatively little heart rot in some species, such as redwood (*Sequoia sempervirens* (D. Don) Endl.), which has great potential longevity. Or, when one or two fungal pathogens have become highly adapted to growth in such hosts, and presumably are tolerant of or able to detoxify the anti-fungal compounds, heart rot is extremely common and intensive. This is the case for western redcedar (*Thuja plicata* Donn ex D. Don) in coastal Alaska where more than half of its volume is rotten, 85% of which is caused by two fungi (*Phellinus weirii* (Murr.) Gilbt. and *Ceriporiopsis rivulosa* (Berk. & Curt.) Gilbn. & Ryv.) (Kimmey 1956).

"Pathological Rotation"

Numerous authors report that heart rot in various forest systems only becomes commercially threatening in older stands. In southeast Alaska, for example, conifers less than 100 years old have little decay, but by 200 years, 65% of western

redcedar, 50% of western hemlock, and 20% of Sitka spruce trees contain decay (Kimmey 1956). Farr et al. (1976) reported a significant correlation between tree age and the percentage of decayed wood volume.

The age of a stand when decay losses exceed annual increment was dubbed the "pathological rotation age" by Meinecke (1916). This age varies widely for different tree species and for a single species in different regions. Western hemlock, for example, reaches "unacceptable" decay losses at stand ages of 225 to 275 years in western British Columbia (Buckland et al. 1949) and 100 to 120 years in Idaho and Montana (Weir and Hubert 1918). The less subjective definition of pathological rotation is sometimes used, which is the stand age at which the decay rate is in equilibrium with the volume of wood produced annually (net wood volume produced is zero). Although this concept was developed for even-aged managed forests, it has ecological relevance to other forests. Many old-growth forests of coastal Alaska are probably near or past that equilibrium. Within age classes of trees, young-trees may be producing positive net volumes of wood each year, but many of the larger, older trees likely have decay losses that exceed wood volume produced.

Are Heart Rot Fungi Pathogens?

Clearly, the destruction of sapwood or phloem directly disrupts a tree's physiology and qualifies the causal organism as a pathogen. With the exception of a few heart rot fungi that continue to advance on the sapwood and cambium, however, most colonize only heartwood and injured sapwood. Although the heartwood is composed primarily of dead xylem cells, it contributes structural support—a vital function to large trees. Heart rot fungi may not always directly alter the physiology of a tree, but, by weakening the structural support of wood, they are frequently the cause of death by bole failure, thus also qualifying them as pathogens.

The relationship between heart rot and bole breakage has been frequently documented, although rarely interpreted ecologically. For obvious reasons, tree failure has been of particular interest to those concerned with potentially hazardous trees around recreation areas and homes. Wood decay is the leading cause of tree failure in such areas (Johnson 1981, Hadfield 1976). The

thickness of sound wood in the outer cylinder in trees with a central heart rot determines structural strength. Several models involving tree diameter and remaining sound wood have been designed to predict tree failure (Wagener 1963, Ossenbruggen et al. 1986, Harvey and Hessburg 1992).

Harris (1989) describes "windfirmness" in trees as the force of the wind on the crown and stem acting in opposition to the resistance of the tree to uprooting or breakage. In general, trees become less windfirm as they grow taller and larger because the force exerted on them by wind increases; and as trees become taller, the turning moment increases with the length of the lever arm (i.e., tree height). When a tree leans with the wind, the force of gravity on the crown and stem adds to the turning moment. Stem decay can provide a weak point in the stem which leads to failure through buckling.

The Heart Rot-Bole Breakage-Wound Cycle

Many of the fungi responsible for the considerable level of heart rot in conifers of coastal Alaska are likely spread by infectious spores colonizing large wounds. One such fungus, *F. pinicola*, is extremely common and causes an estimated 73% of cull in Sitka spruce and 22% of cull in western hemlock in coastal Alaska (Kimmey 1956). In British Columbia, wounding is associated with up to 65% of decay in live western hemlock trees (Buckland et al. 1949). Causes of wounds on trees in Alaska include porcupines, bears, beavers, logging, and road building, but falling trees appear to be the most common form of bole injury in western hemlock old-growth forests (Kimmey 1964). Scars are frequently colonized by decay fungi, particularly when wounds are greater than 0.1m^2 in surface area (Wallis et al. 1971).

The volume of decay is strongly correlated with wound size and scar age of western hemlock and Sitka spruce (Wright and Isaac 1956). Vertical and radial development of decay in wounded boles is quite variable and dependent, in part, on the causal fungus. Silverborg and Larsen (1967) measured the vertical spread of decay by *Phellinus pini* to be 0.26 m/yr , which is generally greater than that of various other tree species reported by Boyce (1961). Data from a study in progress on the rate of decay in wounded western hemlock

and Sitka spruce in Alaska suggest that very little decay develops 20 years after wounding and estimates of time from wounding to substantial radial and vertical decay development should be measured in decades (Hennon, unpublished data).

Thus, at some undetermined time after wounding, perhaps as long as a century or more, wood in the bole of the wounded tree may lose sufficient support and fail. As the bole breaks and the tree falls to the ground or lodges in other trees, one or more adjacent trees are likely to be wounded by having a portion of their bark scraped off. The bark of all coastal Alaskan tree species is thin, perhaps as a result of the rarity of fire, and offers little protection against wounding. Besides wounding, falling trees or snags often kill other trees; more than 15% of the mortality in mature and old-growth Douglas-fir stands in the Pacific Northwest consists of trees knocked over, broken, or crushed by falling trees (Franklin et al. 1987).

Assuming equal amounts of decay, trees with wounds and associated decay may be much more likely to experience bole breakage than unwounded trees with a central column of heart rot. Trees with heart rot limited to the central portion of their boles still maintain the integrity of the outer cylinder (Harvey and Hessburg 1992), whereas, trees with a wound and associated decay lose strength on one side. Piirto et al. (1984) examined large fallen giant sequoia trees (*Sequoiadendron giganteum* (Lindl.) Buchholz) and reported 21 of 33 trees had substantial decay in the area of failure. All but one of twenty seven trees with scars and decay fell in the direction of the scarred side.

The wound-invading heart rot fungi may thus be directly involved in causing gaps, probably by "fine-scale" or minor disturbance in which just one or a few trees are killed as described by Spies and Franklin (1989). The largest, oldest trees may be those most frequently affected by heart rot and bole breakage; their death would tend to create a substantial opening in the canopy. Because such a long period of time elapses between the wounding event and sufficient heart rot development to predispose a tree's bole to break, this heart rot-bole breakage-wound cycle (Fig. 1) may not perpetuate a simple expanding canopy gap. Rather, bole breakage occurs long after invasion, other vegetation responses, and canopy reclosure. Thus, gaps could be continually opening and closing in a scattered spatial pattern across the forest landscape.

Consequences of Mode of Death

Ecological studies on gaps should document how trees die because different types of tree mortality affect vegetation response (Putz et al. 1983, Franklin et al. 1987). For example, different opportunities exist for vegetation to respond in gaps where tree crowns thin slowly and trees die standing, compared to those where trees die suddenly by uprooting or bole breakage (Lertzman and Krebs 1991). In coastal Alaska, windthrow of trees by uprooting exposes mineral soil and mixes it with organic layers. This favors the reproduction of Sitka spruce (Deal et al. 1991). Uprooting also creates mounds which are important sites for regeneration and exploitation for both conifers and other vegetation. The decaying boles of uprooted and snapped trees enhance the regeneration of hemlock by serving as nurse logs (Ruth and Harris 1975, Harmon and Franklin 1989), but how previous heart rot in logs affects this regeneration is not known. Perhaps heart rot makes logs suitable for tree colonization more quickly but, because they are partially decomposed before tree death, these logs may not be as persistent as logs from living trees that had no heart rot. Uprooted trees and trees that die with broken boles usually fall to the ground and decay in place, slowly sinking into the forest floor. Trees that die and partially decompose standing finally fall to the ground and shatter, frequently scattering fragments of decayed wood across the forest floor (Hennon and Loopstra 1991).

The type of decay caused by heart rot fungi, whether white rot or brown rot, has ecological significance. Both types of decay occur in stages, first as a visible stain with little-to-no loss of wood strength followed by advanced decay with substantial loss of strength. The "white rot fungi" produce enzymes that diffuse relatively short distances, but enable them to degrade all major components of the cell walls of wood, sometimes resulting in pockets of decay surrounded by sound wood. In the late stages of some white rots, tree boles become entirely hollow. The "brown rot fungi," however, remove cellulose and hemicellulose from wood, but do not decompose lignin. Wood attacked by the brown rot fungi loses almost all of its strength, but persists as cubical pieces composed primarily of partially modified lignin. Brown rot residues are extremely stable and provide important properties to the organic compo-

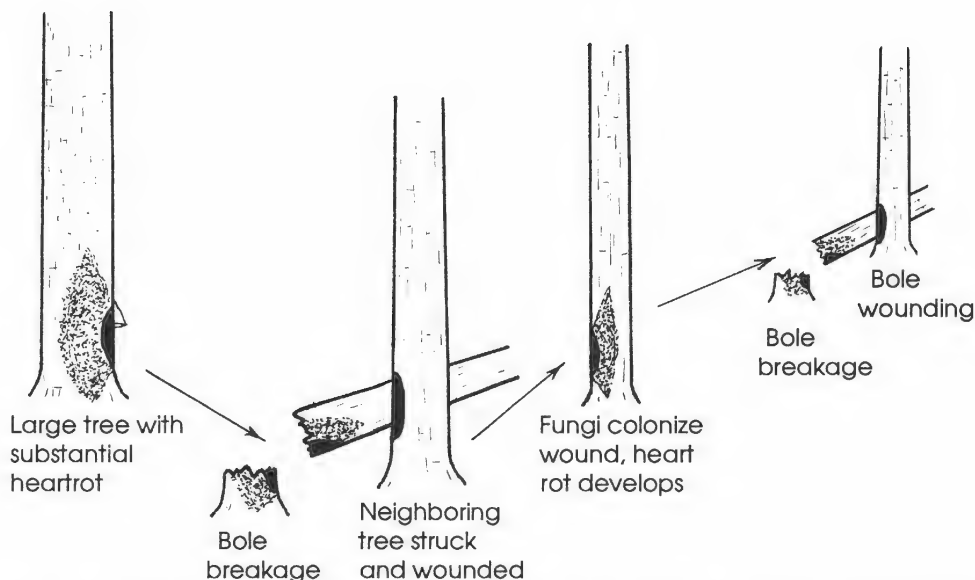


Figure 1. The hypothetical heart rot-bole breakage-wound cycle. Large, old trees frequently contain substantial amounts of heart rot in coastal Alaska. They are predisposed to die by bole breakage and frequently cause bole wounds on adjacent trees. The thin bark and decay-susceptible wood of coastal tree species offers little protection. Heart rot fungi colonize wood in the exposed wound and, long after the wounding event, these trees have developed enough heart rot to also succumb to bole breakage. The time required between bole wounding and the development of substantial heart rot suggests that this process of disturbance would result in small canopy gaps opening and closing in a dispersed spatial pattern.

nent of forest soils (Gilbertson and Ryvarden 1986) where they may comprise up to 30 per cent of soil volume in the upper layers (McFee and Stone 1966). Nitrogen fixation is performed by various soil microorganisms in brown-rotted wood which leads to an important nutrient source for vegetation and their mycorrhizal symbionts (Larsen et al 1982). Nitrogen fixation has also been demonstrated in heart rot columns of live trees, including several combinations of tree and fungal species that occur in Alaska (Harvey et al. 1989). Thus, higher levels of nitrogen in live trees with heart rot may influence ecological processes after these trees die.

Ugolini and Mann (1979) suggest that old forests in coastal Alaska eventually convert to bogs if they persist for very long periods of time without a disturbance that causes soil mixing. Gradually, trees die as soil layers accumulate that restrict moisture drainage (i.e., paludification) and forest floor organic matter increases, tying up nutrients and oxygen. The mode of tree death (soil mixing from uprooting or without soil mixing from

bole breakage or trees dying upright) may affect the future productivity and direction of succession. Disturbance caused by heart rot fungi may contribute negatively to the long-term productivity of such sites. Whether paludification is occurring region-wide and bogs are the "climax" condition are not known (Harris and Farr 1974).

Heart Rot Fungi and Recent Gap-Phase Studies

Most studies on gaps have investigated the vegetation response to disturbance, but have not thoroughly examined causes of gap formation. Several recent studies, however, have documented different mortality causes of canopy-level trees. In a study of gap-dynamics of *Acer-Fagus* forests in Ohio, for example, Runkle (1990) described that gaps are caused in roughly equal numbers by trees being uprooted, broken off low (<2.5m) or broken off high. The very largest trees tended to die by bole breakage, but no mention of the presence of heart rot was made. Dead standing

trees were the most common gapmakers followed by trees with bole breakage and then uprooting in a subalpine forest in British Columbia (Lertzman and Krebs 1991). Putz et al. (1983) described the frequency of uprooting and bole breakage of trees in gap formation of a rainforest in Panama. Bole breakage accounted for 70% of fallen trees, but only 13% of these had heart rot, thus illustrating that tree boles can break without having heart rot. Bole breakage in this example was associated with tree species with low density, weak wood.

Bole breakage of old-growth overstory trees accounted for 30% and 19% of mortality in Douglas-fir and western hemlock, respectively, in Oregon and Washington (Spies et al. 1990). Associated heart rot was not discussed but, elsewhere, Franklin et al. (1987) described that a large percentage of windthrown old-growth Douglas-fir contain substantial butt rot by the decay fungus *Phaeolus schweinitzii*. Gratkowski (1956) did not distinguish between uprooting and bole breakage when discussing windthrow of old-growth Douglas-fir near cutting boundaries in Oregon, but the author did note that root rots (caused primarily by *Phellinus weirii*) and butt rots (caused primarily by *Phaeolus schweinitzii*) were associated with 34% and 20% of windthrow, respectively. Breakage high on boles accounted for only 5% of windthrown Douglas-fir, but every affected tree had advanced heart rot caused by *P. pini*. Holah et al. (1993) determined that root disease-mortality (caused by *Phellinus weirii*) initiated considerable change in the composition of plant communities in old-growth Douglas-fir forests in Oregon. Several root and butt rot fungi, including *P. weirii*, are likely important disturbance agents in coniferous forests of British Columbia (van der Kamp 1991) where they enhance biological diversity.

In a gap-phase forest in Japan, Kanzaki (1984) found heart rot to be more common in *Abies* spp., where it apparently led to high mortality, compared to *Tsuga diversifolia* (Maxim.) Masters. Kanzaki (1984) concluded that the "life-span" of some species in Japan may be determined by heart rot but the causal fungi or incidence of bole breakage were not reported. In a study on the causes of forest gaps at various elevations in New Hampshire (Worrall and Harrington 1988), diseases were responsible for up to 66% of the gap area with several species of root and butt rot fungi contribut-

ing to this disturbance at low elevations, primarily by bole breakage.

Heart Rot Fungi, Diversity, Stability, and Wildlife Habitat

Decay fungi, as members of the flora present, contribute directly to biological diversity of forests. Basidiocarps (conks) of some heart rot fungi are commonly collected as edibles (e.g., *L. sulphureus*) and at least one has been gathered because of its medicinal use (e.g., *Fomitopsis officinalis* (Vill.:Fr.) Bond. et Sing.). The latter fungus was also collected by Native shamens in coastal Alaska because it was thought to contain supernatural powers. The basidiocarps were carved into figures and, known as "bread of ghosts," were used in rituals and as the guardians of grave sites (Blanchette et al. 1992).

The old-growth phase of forests in coastal Alaska has extreme variation in vertical and horizontal structure (Alaback 1982). Heart rot fungi may contribute to maintaining this diverse phase by aiding in its development and stability. Frequent, small-scale disturbance (e.g., bole breakage gaps) may reduce the likelihood of large-scale pest epidemics because no single age group or stress group is widely represented as would be the case in a more homogenous forest. Along with the other forms of mortality, heart rot fungi contribute to the variety of snags, completely uprooted trees with their resulting associated pit and mound topography, and the stump-like lower bole of broken trees and hollow logs on the forest floor.

By increasing the variability of structure in forests, heart rot fungi indirectly enhance habitat for many wildlife species. Mortality factors of large trees that open the canopy and allow more light to reach the forest floor are beneficial to wildlife species that feed on understory vegetation, such as black-tailed deer in southeast Alaska (Taber and Hanley 1979).

Wood decay fungi initiate a complex succession of organisms in logs and standing boles that range from saprophytic microorganisms (some of which fix nitrogen), invading plants and their mycorrhizal fungi, animal herbivores and fungivores, omnivores, to many predators including vertebrates such as salamanders, bats, and bears (Maser et al. 1988). Heart rot fungi speed access to tree boles because many organisms, large and small, rely on the creation of open, internal spaces

in wood (Maser et al. 1988). Heart rot fungi are critically important for cavity nesting birds. Wood decay in trees is an essential precursor to use by cavity excavators (McClelland and Frissell 1975). Large trees that contain heart rot before they die may be particularly important to cavity-nesting birds because these trees may be used by primary excavators before and long after tree death.

Conclusions

Old hemlock-spruce forests of coastal Alaska have large quantities of heart rot. Many of these forests appear to be functioning by gap development between the long periods of episodic large-scale disturbances. Heartrot fungi may also contribute to large-scale disturbance; Harris (1989) suggested that catastrophic windthrow is more common in stands containing heartrot. Uprooted trees, trees with broken boles, and dead standing trees all appear to be common and seem to be initiating or continuing the development of gaps, perhaps in combination with one another. But until we gather such data, we will not have an understanding of what factors, alone or in combination, drive the gap-dynamic process of these forests.

Ecological studies on gaps should consider the disturbance role of heart rot fungi by determining the incidence of uprooted trees, trees whose boles break, and trees that die standing—all with and without the presence of heart rot. Comparisons should be made with the level of heart rot in

surviving, standing trees. Identifying heart rot fungi to species in these gaps will convey additional information on spatial relationships because we have knowledge of how some of these fungi spread within and among trees. For example, several of the root and butt rot fungi spread along root systems and kill adjacent trees in groups. Comparing the incidence of different gapmakers with site environmental variables may indicate that some sites favor heart rot and bole breakage while on other sites uprooting or standing death may be more common in gap development. Sites with soils that allow deeper rooting and thus greater resistance to uprooting (Putz et al. 1983), for example, may have relatively more bole breakage.

Although there are some apparent differences, the temperate rainforests of coastal Alaska may share a similar pattern of forest development with rainforests in the tropics and subtropics where large-scale disturbance is also infrequent. Perhaps the importance of pathogens, and heart rot fungi in particular, has been overlooked or downplayed in many of these gap-dynamic forests. Working together, ecologists, pathologists, and mycologists can contribute significantly to our understanding of disturbance ecology by investigating the causes as well as the consequences of tree mortality in studies on forest canopy gaps.

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Literature Cited

- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. *Ecology* 63: 1932-1948.
- . 1988. Dynamics of old-growth temperate rainforests in southeast Alaska. *Proceedings of Glacier Bay Science Symposium* 2: 150-153.
- Blanchette, R. A., B. D. Compton, N. J. Turner, and R. L. Gilbertson. 1992. Nineteenth Century Shaman grave guardians are carved *Fomitopsis officinalis* sporophores. *Mycologia* 84: 119-124.
- Boyce, J. S. 1961. *Forest pathology*. McGraw-Hill, New York. 572p.
- Boyce, J. S., and J. W. B. Wagg. 1955. Conk rot of old-growth Douglas-fir in western Oregon. *Oregon Forest Products Lab. Bull.* 4: 1-96.
- Buckland, D. C., R. E. Foster, and V. J. Nordin. 1949. Studies in forest pathology. VII. Decay in western hemlock and fir in the Franklin River area, British Columbia. *Can. J. Res. Sect. C* 27: 312-331.
- Deal, R. L., C. D. Oliver, and B. T. Bormann. 1991. Reconstruction of mixed hemlock-spruce stands in coastal Alaska. *Can. J. For. Res.* 21: 643-654.
- Etheridge, D. E. 1972. True heartrots of British Columbia. *Can. For. Ser., Pac. For. Res. Cen., Victoria, British Columbia. Forest Pest Leaflet No. 55* 14p.
- . 1973. Wound parasites causing tree decay in British Columbia. *Can. For. Ser., Pac. For. Res. Cen., Victoria, British Columbia. Forest Pest Leaflet No. 62* 15p.
- Etheridge, D. E., and H. M. Craig. 1976. Factors influencing infection and initiation of decay by the indian paint fungus (*Echinodontium tinctorium*) in western hemlock. *Can. J. For. Res.* 6: 299-318.
- Farr, W. A., V. J. LaBau, and T. H. Laurent. 1976. Estimation of decay in old-growth western hemlock and Sitka spruce in southeast Alaska. *USDA For. Ser., Pac. Northwest For. and Range Exp. Sta., Portland OR. Research Paper PNW-204*. 24p.

- Foster, R. E., H. M. Craig, and G. W. Wallis. 1954. Studies in forest pathology. XII. Decay of western hemlock in the upper Columbia Region, British Columbia. *Can. J. Bot.* 32: 145-171.
- Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. *Bioscience* 37:550-556.
- Gilbertson, R. L., and L. Ryvarden. 1986. North American Polypores, Volume 1. Fungiflora, Oslo. 433p.
- Gratkowski, H. J. 1956. Windthrow around staggered settings in old growth Douglas-fir. *Forest Science* 2: 60-74.
- Haddow, W. R. 1938. The disease caused by *Trametes pini* (Thore) Fries in white pine (*Pinus strobus* L.). *R. Can. Inst. Trans.* 47: 21-80.
- Hadfield, J. S. 1976. Judging potential for failure in western hemlock and Sitka spruce. Pp. 27-30. In: Russell, K., ed., Proceedings, 24th annual western international forest disease work conference; Sep. 13-17, 1976. Coos Bay, Or. Olympia, WA. Dep. Nat. Res. 151p.
- Harmon, M. E., and J. F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70: 48-59.
- Harris, A. S. 1989. Wind in the forests of southeast Alaska and guides for reducing damage. USDA For. Ser., Pac. Northwest Res. Sta., Portland, OR., Gen. Tech. Rep., PNW-GTR-244. 63p.
- Harris, A. S., and W. A. Farr. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Ser., Pac. For. Res. Sta., Portland, OR., Gen. Tech. Rep. PNW-25. 109p.
- Hartig, R. 1874. Wichtige Krankheiten der Waldbäume. Beiträge zur Mycologie und Phytopathologie für Botaniker und Forstmänner. Berlin, Springer. 127p.
- Harvey, A. E., M. J. Larsen, M. F. Jurgensen, and E. A. Jones. 1989. Nitrogenase activity associated with decayed wood of living Northern Idaho conifers. *Mycologia* 81: 765-771.
- Harvey, R. D., and P. F. Hessburg. 1992. Long-range planning for developed sites in the Pacific Northwest: the context of hazard tree management. USDA Forest Service, Portland OR. FPM-TP-039-02. 120p.
- Hennon, P. E., and E. M. Loopstra. 1991. Persistence of western hemlock and western redcedar trees 38 years after girdling at Cat Island in southeast Alaska. USDA For. Ser., Pac. Northwest Res. Sta., Portland, OR. Res. Note PNW-RN-507. 5p.
- Hennon, P. E., R. Mask, and E. H. Holsten. 1994. Insect and disease conditions in Alaska, 1994. USDA For. Ser., Anchorage, AK. Gen. Tech. Rep. R10-TP-51. 42p.
- Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. USDA For. Ser., Washington, D.C., Agric. Handb. No. 386. 658p.
- Holah, J. C., M. V. Wilson, and E. M. Hansen. 1993. Effects of a native forest pathogen, *Phellinus weirii*, on Douglas-fir forest composition in western Oregon. *Can. J. For. Res.* 23: 2473-2480.
- Holsten, E. H., P. E. Hennon, and R. A. Werner. 1985. Insects and diseases of Alaskan forests. USDA For. Ser., Anchorage AK., Alaska Region Rep. No. 181. 217p.
- Johnson, D. W. 1981. Tree hazards, recognition and reduction in recreation areas. USDA For. Ser., Forest Pest Management, Denver. Tech. Rep. R2-1. 16.
- Kanzaki, M. 1984. Regeneration in subalpine forests I. Mosaic structure and regeneration process in a *Tsuga diversifolia* forest. *Bot. Mag. Tokyo* 97: 297-311.
- Kile, G. A., G. I. McDonald, and J. W. Byler. 1991. Ecology and disease in natural forests. Pp. 102-121. In: *Armillaria* root disease, Eds. C. E. Shaw III and G. A. Kile, USDA For. Ser., Washington, D.C., Agric. Handbk. No. 691. 233p.
- Kimney, J. W. 1956. Cull factors for Sitka spruce, western hemlock and western redcedar in southeast Alaska. USDA For. Ser., Alaska For. Res. Cent., Juneau, AK. Station Paper No. 6. 31p.
- Kimney, J. W. 1964. Heart rots of western hemlock. USDA For. Ser., Washington. For. Pest Leaflet 90. 7p.
- Larsen, M. J., M. F. Jurgensen, and A. E. Harvey. 1982. N₂ fixation in brown-rotted soil wood in an Intermountain cedar-hemlock ecosystem. *Forest Sci.* 28: 292-296.
- Lertzman, K. P., and C. J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Can. J. For. Res.* 21: 1730-1741.
- Maser, C., S. P. Cline, K. Cromack, Jr., J. M. Trappe, and E. M. Hansen. 1988. What we know about large trees that fall to the forest floor. Pp. 25-45. In: Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds. From the forest to the sea: a story of a fallen tree. USDA For. Ser., Portland, OR., Gen. Tech. Rep. PNW-GTR-229. 153p.
- McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. *J. of Forestry* 73: 414-417.
- McFee, W. W., and E. L. Stone. 1966. The persistence of decaying wood in the humus layers of northern forests. *Proc. Soil Sci. Am.* 30: 513-516.
- Meinecke, E. P. 1916. Forest pathology in forest regulation. *USDA Bull.* 275: 1-63.
- Oliver, C. D., and B. C. Larson. 1990. Forest stand dynamics. McGraw Hill, New York. 467p.
- Ossenbruggen, P. J., M. A. Peters, and A. L. Shigo. 1986. Potential failure of a decayed tree under wind loading. *Wood and Fiber Science* 8: 168-186.
- Owens, C. E. 1936. Studies on the wood-rotting fungus, *Fomes pini*. I. Variations in morphology and growth habit. *Amer. J. Bot.* 23: 144-149.
- Piirto, A. U., D. D. Wilcox, W. W. Parmeter Jr., and D. L. Wood. 1984. Causes of uprooting and breakage of specimen giant sequoia trees. Univ. California, Berkeley, CA., Div. Agric. and Natural Resources Bull. No. 1909. 14p.
- Putz, F. E., P. D. Coley, K. Lu, A. Montalvo, and A. Aiello. 1983. Uprooting and snapping of trees; structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011-1020.
- Runkle, J. R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.* 20: 632-641.
- Ruth, R. H., and A. S. Harris. 1975. Forest residues in hemlock-spruce forests of the Pacific Northwest and Alaska. USDA For. Ser., Pac. Northwest Res. Sta., Portland, OR. Gen. Tech. Rep. PNW-39.
- _____. 1979. Management of western hemlock-Sitka spruce forests for timber production. USDA For. Ser., Pac. Northwest Res. Sta., Portland, OR. Gen. Tech. Rep. PNW-88.

- Shigo, A. L. 1967. Succession of organisms in discoloration and decay of wood. *Int. Rev. For. Res.* 2: 237-299.
- Silberborg, S. B., and M. J. Larsen. 1967. Rate of decay in *Pinus strobus* following artificial inoculation with *Fomes pini*. *Plant Disease Repr.* 51: 829-831.
- Spies, T. A., and J. F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology* 70:543-545.
- Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20: 649-658.
- Taber, R. D., and T. A. Hanely. 1979. The black-tailed deer and forest succession in the Pacific Northwest. Pp. 33-52. In: Sitka black-tailed deer: proceedings of a conference. Eds.: Wallmo, O. C. and J. W. Schoen, USDA For. Ser., Juneau AK.
- Ugolini, F. C., and D. H. Mann. 1979. Biopedological origin of peatlands in southeast Alaska. *Nature* 281: 366-368.
- Van der Kamp, B. J. 1991. Pathogens as agents of diversity in forested landscapes. *Forest Chron.* 67: 353-354.
- Wagener, W. W. 1963. Judging hazard from native trees in California recreation areas: —a guide for professional foresters. USDA For. Ser. Res. Pap., PSW-P1. 29p.
- Wallis, G. W., G. Reynolds, and H. M. Graig. 1971. Decay associated with logging scars on immature western hemlock in coastal British Columbia. For. Res. Lab., Victoria, B.C., Canada. Information Report BC-X-54. 8p.
- Weir, J. R., and E. E. Hubert. 1918. A study of heart-rot in western hemlock. U.S. Dep. Agr. Bull. 722:1-37.
- Worrall, J. J., and T. C. Harrington. 1988. Etiology of canopy gaps in spruce-fir forests at Crawford Notch, New Hampshire. *Can. J. For. Res.* 18: 1463-1469.
- Wright, E., and L. A. Isaac. 1956. Decay following logging injury to western hemlock, Sitka spruce, and true firs. USDA For. Ser., Washington, D.C. Tech. Bull. No. 1148. 34p.

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Down Logs as Habitat for Forest-dwelling Ants—the Primary Prey of Pileated Woodpeckers in Northeastern Oregon

Abstract

Logs on the forest floor in 240 sample plots in the Blue Mountains of northeastern Oregon were counted and their physical characteristics described in relation to ant colonization. The plots were located in 12 home ranges of pileated woodpecker (*Dryocopus pileatus* (L.)), a Management Indicator Species in USDA Forest Service management guidelines. One or more species of ants were found in 62% of 1,385 sectioned logs. Of 13 species of ants found, the most common were *Lasius alienus* (Foerster), *Formica neorufibarbis* Emery, and *Camponotus modoc* (Wheeler). Wood-dwelling ants that colonize down logs and snags are the primary prey for pileated woodpecker. Relationships between physical characteristics and species of down logs, their colonies of ants, and foraging pileated woodpeckers are discussed. Differential occurrences among genera and species of ants suggest a complex picture of species, sizes, and stages of decay of logs chosen for colonization. The relationships of logs and ants to management of pileated woodpecker and to western spruce budworm (*Choristoneura occidentalis* (Freeman)), a major forest-defoliating insect, are also explored.

Introduction

Down logs are an important colonizing substrate for forest-dwelling ants. Although these ants are a largely ignored component in mixed-conifer stands of the Pacific Northwest, they play important roles in ecosystem function. They are actively involved in decomposition of dead wood, nutrient cycling, plant pollination, seed dispersal, and predation upon insects. In addition, ants are the prey for other arthropods and wildlife species in the forest (Petal 1978, Youngs 1983, Holldobler and Wilson 1990, Way and Khoo 1992). Maser and Trappe (1984) and Hall and Thomas (1984) recognized the importance of ants in Pacific Northwest forests, but little work has been done to clarify ecological associations between ants and other forest-dwelling vertebrates and invertebrates. Notable exceptions are studies describing relationships between ants and the pileated woodpecker (*Dryocopus pileatus* (L.)) (Beckwith and Bull 1985, Bull et al. 1992), and between ants and the western spruce budworm (*Choristoneura occidentalis* (Freeman)) (Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984).

Bull et al. (1992) reported that *Camponotus* and *Formica* ants are the principal food for pileated woodpeckers in northeastern Oregon, where they comprised about 97% of the woodpecker's diet as represented in 330 scat samples gathered year-

round. The pileated woodpecker is a large, tree-cavity excavator that is ecologically tied to old-growth mixed-conifer stands. This association is principally a result of the woodpecker's need for large dead trees for nesting, large hollow trees for roosting, and abundant standing and down dead wood for foraging (Bull and Holthausen 1993).

Because pileated woodpecker populations can be adversely affected by management activities that reduce the number of large trees (Bull and Meslow 1977), this bird was selected by the USDA Forest Service as a Management Indicator Species (U.S. Laws, Statutes, etc. 1976). Under this designation, National Forests in the Pacific Northwest Region must be managed to provide habitat to maintain viable populations of pileated woodpecker within its natural range.

Toward this goal, the USDA Forest Service has developed various sets of standards and guidelines in each of several National Forests to provide adequate nesting areas. Less attention, however, has been given to requirements for foraging habitat. Current guidelines provide for foraging areas of about 120 ha but do not address specifically the amounts, species, or size classes of down logs where 38% of foraging occurs (Bull and Holthausen 1993). No studies have addressed the arthropod community residing in snags where another 38% of foraging by the woodpecker occurs. This is possibly either because of the need

to destructively sample the limited number of snags, or the risks involved in falling the snag, or in climbing and sampling.

In addition to being an important food source for pileated woodpecker, ants are predators of the western spruce budworm (Youngs and Campbell 1984, Torgersen et al. 1990). Populations of this important forest insect sporadically erupt into outbreaks in mixed-conifer stands throughout the West, where the larvae may defoliate trees (Brookes et al. 1987). Of the 13 species of ants that prey on the budworm, 12 species colonize standing or down dead wood (Smith 1979; R.D. Akre, Washington State University, Pullman, Wash., personal communication). Unfortunately, little is known about the frequency of occurrence of forest-ant colonies, or about the size, species, and physical characteristics of the logs in which they occur.

Because down wood plays an important role as habitat for these ants, whose numbers influence those of both the pileated woodpecker and western spruce budworm (Figure 1), we undertook this study. Our specific objectives were to (1) describe the number, size, species, and other physical characteristics of logs used by forest-dwelling ants in home ranges of pileated woodpeckers; and (2) identify and determine the rela-

tive frequency of the species of ants that used those logs.

Methods

Study Sites

We used 12 study areas, each delineated by the home range of a pair of pileated woodpeckers. These home ranges, which averaged 597 ha (range 200-1464 ha), were in the Blue Mountains of northeastern Oregon in Baker, Union, and Wallowa Counties (Bull and Holthausen 1993). Forested areas within the home ranges were predominantly uneven-aged mixed-conifer stands of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.); Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco); ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.); western larch (*Larix occidentalis* Nutt.); and lodgepole pine (*Pinus contorta* Dougl. ex Loud.).

Aerial photographs with sketched boundaries of each home range were used to define the study areas. Twenty sampling points per home range were systematically selected by using a grid overlaid on the aerial photos. Points falling in nonforested, grassy openings were relocated to the nearest grid-point in a forested area. When a

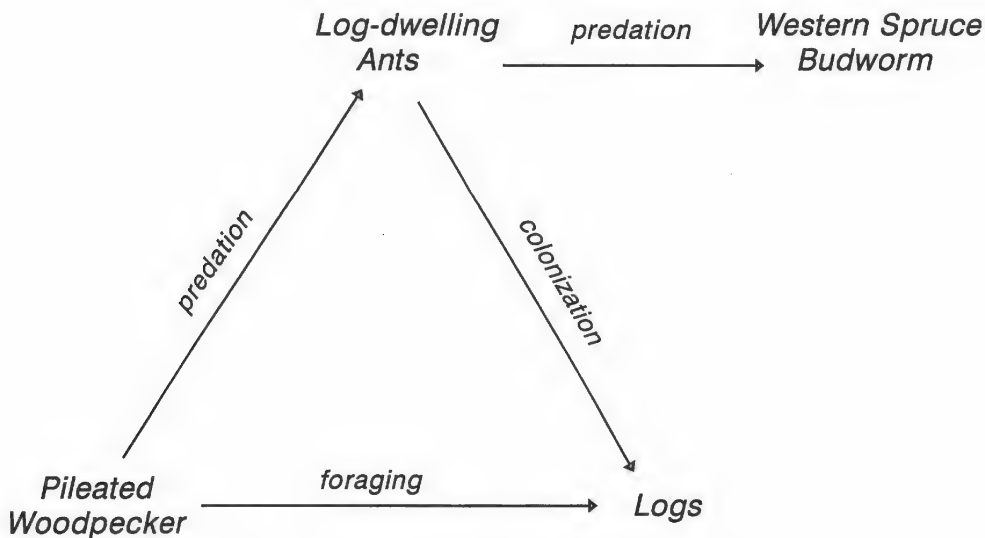


Figure 1. Diagram showing functional relationships between log-dwelling ants, logs, pileated woodpecker, and western spruce budworm in northeastern Oregon.

sample point shown on an aerial photo was located on the ground, that point became the SW corner of a 20- X 20-m plot laid out in cardinal directions.

Sampling

Log sampling was done between 24 May and 25 June 1991. In each plot, all logs ≥ 15 cm in diameter at the large end and ≥ 2 m long were measured and described. A 15-cm large-end diameter of logs was chosen based on field observations by the junior author, who found few signs of pileated woodpecker foraging in logs below this minimum. The 2-m minimum length was based on our judgment that shorter logs did not provide suitable habitat for ants, and on constraints of available time and labor. Recorded log measurements included length within the plot, and large- and small-end diameters 10 cm from each end or where the log crossed the plot boundary. The large-end diameter of butt logs with some of the root wad present were measured just distad of the butt swell. Logs were classified by large-end diameter into four categories that approximate the classes for diameter at breast height (DBH) of standing trees used by the Forest Service (USDA Forest Service 1985). These classes are: 15-22 cm (6.0-8.9 in.) for poles; 23-37 cm (9-14.9 in.) for small logs, 38-50 cm (15.0-19.9 in.) for medium-sized logs; and ≥ 51 cm (≥ 20 in.) for large logs. Mean log diameter was obtained by aver-

aging the large- and small-end diameters. Volume of logs was calculated by using the length of the log and its mean diameter to compute the volume of the log as a cylinder.

Species of each log was recorded. About 10% of the logs were devoid of bark or had decayed to the point that species could not be determined, so they were recorded as "unidentifiable." Douglas-fir and grand fir were especially difficult to separate reliably, so they were combined as "firs."

We chose separate classifications to describe external qualities of the entire log and internal qualities of the wood. To describe overall qualities of entire logs, we classified them according to five log-decomposition classes (Maser *et al.* 1979). These describe a range of logs from ones that retained some twigs ≤ 3 cm in diameter and intact bark to those in advanced stages of decomposition that had partly been incorporated into the forest floor (Figure 2).

To describe qualities of internal wood texture and degree of decomposition, we classified the wood condition as sound, moderately decayed, or in advanced decay. The significant distinction here is that "wood condition" refers to the physical properties of the wood at a sectioning cut. Specifically, it is the extent to which the wood has become soft, friable, spongy, or pitted as a result of attack by decay-causing organisms and channelizing by invertebrates. Our wood condi-

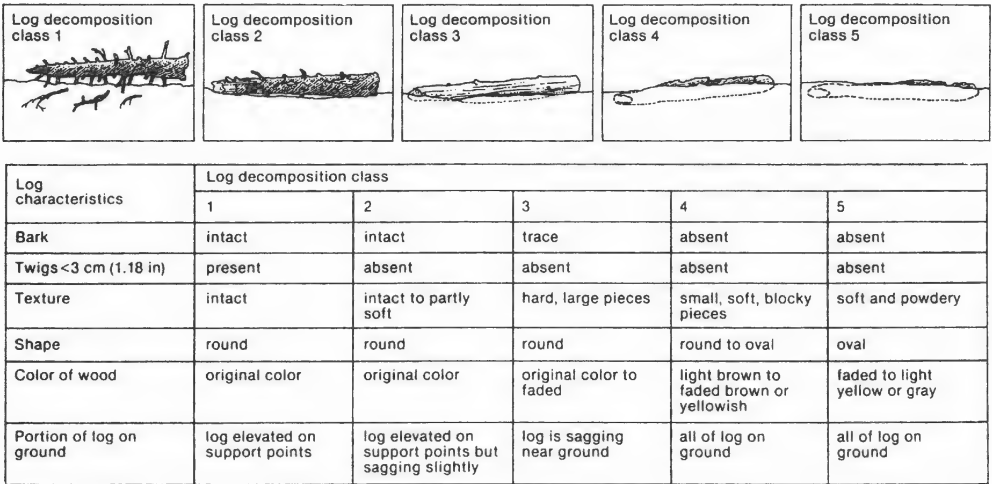


Figure 2. Log decomposition classes (from Maser *et al.* 1979).

tion categories equate with the classes of "internal succession" of Maser et al. (1979).

Ant Collections

To determine the presence of ants within logs, we sectioned six logs per plot with a chainsaw. To assure representation of logs from throughout the plot, we attempted to obtain at least one log from each of the quadrants in the plot. Two logs in each of three diameter-size classes (15-25 cm, 26-40 cm, and >40 cm) were selected for sectioning. Logs were sequentially cut into 1-m lengths beginning 10 cm from the large end or from where the log crossed the boundary of the plot. At sectioning cuts where ants were encountered, we recorded wood condition and whether the log was in contact with the ground.

At each sectioning cut, about 20 specimens of the largest ants (i.e., major workers) were collected and placed into vials containing 70% ethyl alcohol. Each vial was labeled with information on the home range, plot, and log in which the ants were collected. Ants were later identified with the keys of Hansen and Akre (1985) and Wheeler and Wheeler (1986). To confirm identifications, we compared specimens with species verified by D.R. Smith, USDA, ARS, Systematic Entomology Laboratory, U.S. National Museum of Natural History, Washington, DC. Voucher collection is stored at the Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, La Grande, Oregon 97850.

Statistical Analyses

For analysis, species of *Camponotus* and *Formica* were each tallied as a separate group. Species in the genera *Lasius*, *Tapinoma*, *Leptothorax*, and *Aphaenogaster* were grouped and referred to as "Other". Thus, three groups are treated here - *Camponotus*, *Formica*, and Other. Except where noted, when an ant group was found more than once in a log, it was counted only once—i.e., as a single colony. Ants form large colonies that are aggressive toward other ants—even other ants of the same species. Thus, we assumed that ants of the same species that occurred in a single log belonged to the same colony.

Statistical analyses were based on the percentage occurrence of *Camponotus*, *Formica*, or Other ants in sampled logs of a given variable—e.g., log species, large-end diameter class, etc.—in the

home range of each pair of pileated woodpeckers. Standard errors of percentage occurrences were based on 12 home ranges. One-way analysis of variance (ANOVA) (Snedecor and Cochran 1980) was used to determine if the classes of selected variables for sectioned logs were used equally by each ant group. When ANOVA showed that mean percentage occurrences were statistically different ($P \leq 0.05$), we used Tukey's multiple comparisons (Miller 1981) to determine which classes within a variable were statistically different. The variables compared were log species, large-end diameter, length, log-decomposition class, wood condition, and log-contact with the ground. Chi-square analysis was used to test whether the presence or absence of one ant group in a log influenced the presence or absence of another group. Chi-square analyses were also used to determine if the pattern of usage of a given variable differed among ant groups. Stepwise discriminant analysis was used to determine which were the significant predictor variables for each group (SAS 1988). Statistical significance throughout was set at $P \leq 0.05$.

Results

Characteristics of All Logs Sampled

There were 2,779 logs ($\bar{x}$ = 289.5 logs per ha) on the 9.6 ha within the 240 sample plots in the 12 pileated woodpecker pairs' home ranges. Douglas-fir and grand fir (combined as "firs") dominated among the logs (32.4%), but the most common single identifiable species was ponderosa pine (25.7%). Lodgepole pine was more common than larch (17.9% vs. 13.9%), but it also showed more variation in occurrence among the 12 home ranges (standard errors of 5.4% vs. 1.6%) (Table 1).

Nearly half (46.2%) of the logs were in the smallest of the four diameter classes (15-22 cm), representing only 11.9% of the volume (13.2 m³). Conversely, 8.3% of the logs were in the largest diameter class (51-120 cm), but they represented 37.6% of the volume (41.6 m³) (Table 2). The mean large-end diameter was greatest for larch (32.3 $\pm$ 0.8 cm) and smallest for lodgepole pine (22.7 $\pm$ 0.3 cm). The mean large-end diameter for all species of logs was 28.9 $\pm$ 0.3 cm. The mean length for all logs, calculated by using both entire logs and the portions of logs within the plots, was 6.4 $\pm$ 0.04 m; maximum length was 14 m.

TABLE 1. Number and proportional representation of species of logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991.

Species of log	n	Occurrence	Large-end Diameter
		% $\pm$ SE ^a	$\bar{x} \pm$ SE (cm)
Ponderosa pine	673	25.7 $\pm$ 6.2	30.3 $\pm$ 4.10
Firs ^b	841	32.4 $\pm$ 4.1	29.9 $\pm$ 4.30
Lodgepole pine	611	17.9 $\pm$ 5.4	22.7 $\pm$ 2.17
Larch	360	13.9 $\pm$ 1.6	32.3 $\pm$ 4.30
Other spp. ^c	16	0.5 $\pm$ 0.4	24.1 $\pm$ 1.93
Unidentifiable	278	9.6 $\pm$ 2.1	32.0 $\pm$ 4.19
Total	2779		

^a Standard error based on 12 pileated woodpecker home ranges.

^b Douglas-fir and grand fir were combined as "Firs" because of difficulties in identifying decayed logs of these species.

^c Englemann spruce, *Picea engelmannii* Parry ex Engelm., and black cottonwood, *Populus trichocarpa* Torr. & Gray.

Occurrence of Ants

In all, 1,385 logs were cut into 3,221 sections. One or more ant groups were found in 855 (61.8%) of the logs. In these ant-inhabited logs, ants were encountered at 1,063 of the 1,988 sectioning cuts.

Thirteen species of ants were collected from sectioned logs. The most common species encountered were *Lasius alienus*, *Formica neorufibarbis*, and *Camponotus modoc*, which were found in 58% of the sampled logs and comprised 75% of 1,063 occurrences. Overall, the most common species was *Lasius alienus*, which represented 43% of all occurrences of ants. *Formica neorufibarbis* (18%) was only slightly more common than *C. modoc* (14%)(Table 3).

The *Camponotus* were least often associated with another group. The least common combination of groups was the occurrence of *Camponotus* and *Formica* in a single log (Table 4). Chi-square (X^2) analysis indicated that the presence of both *Camponotus* and *Formica* in a log occurred statistically less often than expected ($X^2 = 8.12$, 1 df; $P = 0.0044$). The occurrence of *Camponotus* had no significant influence on the likelihood that the Other group would be present in the same log ($X^2 = 3.20$, 1 df; $P = 0.0736$). On the contrary, the occurrence of *Formica* in a log was positively related to the occurrence of Other ants ($X^2 = 8.97$, 1 df; $P = 0.0027$) there.

Characteristics of Logs Preferred by Ants

Species. Species of logs were used in statistically different proportions only by the *Camponotus* ($P = 0.0016$). Specifically, *Camponotus* occurred in larch logs in significantly greater proportion than in lodgepole pine (Figure 3A). Chi-square analysis to test whether *Camponotus*, *Formica*, and Other ants occupied species of logs in the same proportions revealed no statistically significant differences in occupancy of logs by the three groups.

Large-end Diameter. Size class of logs used for colonization appeared to be important only to *Camponotus* ($P \leq 0.0001$), which occurred more commonly in the largest diameter class (51-120 cm) than in the smallest class (15-22 cm) (Figure 3B). This pattern of occurrence of *Camponotus* was statistically different than occurrence of either *Formica* ($X^2 = 16.32$, 3 df; $P = 0.0010$) or Other ants ($X^2 = 24.18$, 3 df; $P < 0.0001$), which occurred more uniformly among size classes of logs.

TABLE 2. Number and volume of logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991

Large-end diam. size class (cm)	Total no. of logs	Logs per ha $\bar{x} \pm$ SE ^a	Volume per log (m ³) $\bar{x} \pm$ SE	Volume per ha (m ³) $\bar{x} \pm$ SE
15-22	1284	133.7 $\pm$ 17.8	0.0985 $\pm$ 0.0035	13.2 $\pm$ 0.5
23-37	920	95.9 $\pm$ 6.4	0.3044 $\pm$ 0.0064	29.2 $\pm$ 0.6
38-50	344	35.9 $\pm$ 2.5	0.7275 $\pm$ 0.0268	26.1 $\pm$ 1.0
51-120	231	24.0 $\pm$ 3.2	1.7317 $\pm$ 0.0912	41.6 $\pm$ 2.2
All size classes	2779	289.5 $\pm$ 22.6	0.3826 $\pm$ 0.0112	110.8 $\pm$ 3.2

^a Standard error based on 12 home ranges.

TABLE 3. Frequency of ant species or groups occurring in sectioned logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991

Species of ants	Number of occurrences ^a	% logs $\pm$ SE ^b
<i>Camponotus</i> species		
<i>C. modoc</i> (Wheeler)	151	10.8 $\pm$ 1.1
<i>C. vicinus</i> Mayr	16	1.1 $\pm$ 0.7
<i>C. laevigatus</i> (F. Smith)	6	0.4 $\pm$ 0.2
Unknown	4	0.3 $\pm$ 0.1
Total ^c	177	12.5 $\pm$ 1.6
<i>Formica</i> species		
<i>F. neorufibarbis</i> Emery	195	14.0 $\pm$ 1.6
<i>F. accreta</i> Francoeur	72	5.2 $\pm$ 1.2
<i>F. haemorrhoidalis</i> Emery	6	0.4 $\pm$ 0.2
<i>F. densiventris</i> Viereck	5	0.4 $\pm$ 0.2
<i>F. subnuda</i> Emery	2	0.2 $\pm$ 0.1
<i>F. lasioides</i> Emery	1	0.1 $\pm$ 0.1
Unknown	10	0.7 $\pm$ 0.3
Total ^c	281	20.2 $\pm$ 2.2
Other species		
<i>Lasius alienus</i> (Foerster)	455	32.9 $\pm$ 2.6
<i>Tapinoma sessile</i> (Say)	71	5.2 $\pm$ 1.0
<i>Leptothorax muscorum</i> (Nylander)	45	3.3 $\pm$ 0.9
<i>Aphaenogaster occidentalis</i> (Emery)	24	1.7 $\pm$ 0.7
Total ^c	567	41.1 $\pm$ 3.0

^a Each species or group counted only once per log.

^b Based on 1,385 logs in 12 home ranges.

^c "Total" categories are not simple sums of the tallies for individual species because occurrences of a genus or group are counted only once in a log.

Length. The length of logs influenced the presence of *Formica* and Other ants, both of which showed statistically significant differences in occurrence among the four log-length classes ($P = 0.0155$ and 0.0137 , respectively). Both these groups favored logs ≥ 7 m long over logs that were 1-3 m. *Camponotus* used all the log-length classes about equally ($P = 0.3904$) (Figure 3C). Compared to each other, none of the groups used the log-length classes in statistically different ways (all $X^2 \leq 4.92$, 3 df; all $P \geq 0.1777$).

TABLE 4. Frequencies of occurrence of ant groups alone or in combination with other groups in sectioned logs in 12 home ranges of pileated woodpecker in northeastern Oregon, May-July 1991.

		<i>Formica</i>		Other	
		Yes	No	Yes	No
<i>Camponotus</i>	Yes	21	152	60	113
	No	260	952	507	705
Other	Yes	93	188		
	No	474	630		

Results of Chi-square tests, 1 df - *Camponotus* vs. *Formica*, $X^2 = 8.12$, $P = 0.0040$; *Camponotus* vs. Other, $X^2 = 3.20$, $P = 0.0736$; *Formica* vs. Other, $X^2 = 8.97$, $P = 0.0027$.

Log-decomposition Class. Only *Formica* used the various decomposition classes in significantly different proportions ($P < 0.0001$). In particular, *Formica* occurred significantly less commonly in log-decomposition class 5, the most decomposed logs, than in classes 1-4 (Figure 3D). Overall, the proportions in which *Formica* used logs among the decomposition classes differed from both *Camponotus* ($X^2 = 11.55$, 4 df; $P = 0.0210$) and Other ants ($X^2 = 9.8$, 4 df; $P = 0.0439$).

Ground Contact. Log contact with the ground at the site of occurrence of ants was not a significant factor for either *Camponotus* or *Formica* (Figure 3E), nor did these two groups differ from one another ($X^2 = 0.6800$, 1 df; $P = 0.4096$). However, *Formica* showed a tendency, though non-significant ($P = 0.0700$), to occur in log sections without ground contact. The Other ants showed a clear preference for log sections with ground contact ($P = 0.0166$) (Figure 3E) - opposite of the preference displayed by *Formica* ($X^2 = 7.44$, 1 df; $P = 0.0064$).

Wood Condition. Solid wood supported colonies of *Camponotus* significantly more commonly ($P = 0.0038$) than did wood with moderate or advanced decay (Figure 3F). Neither *Formica* nor the Other ants showed differential preference for a particular wood condition, and both groups differed significantly from *Camponotus* in this regard ($X^2 \geq 35.18$, 2 df; $P < 0.0001$).

Discriminant Analysis

Stepwise discriminant analysis considered the following variables: large- and small-end diameters, log-length, tree species, length x species, log-decomposition class, and ground contact. The

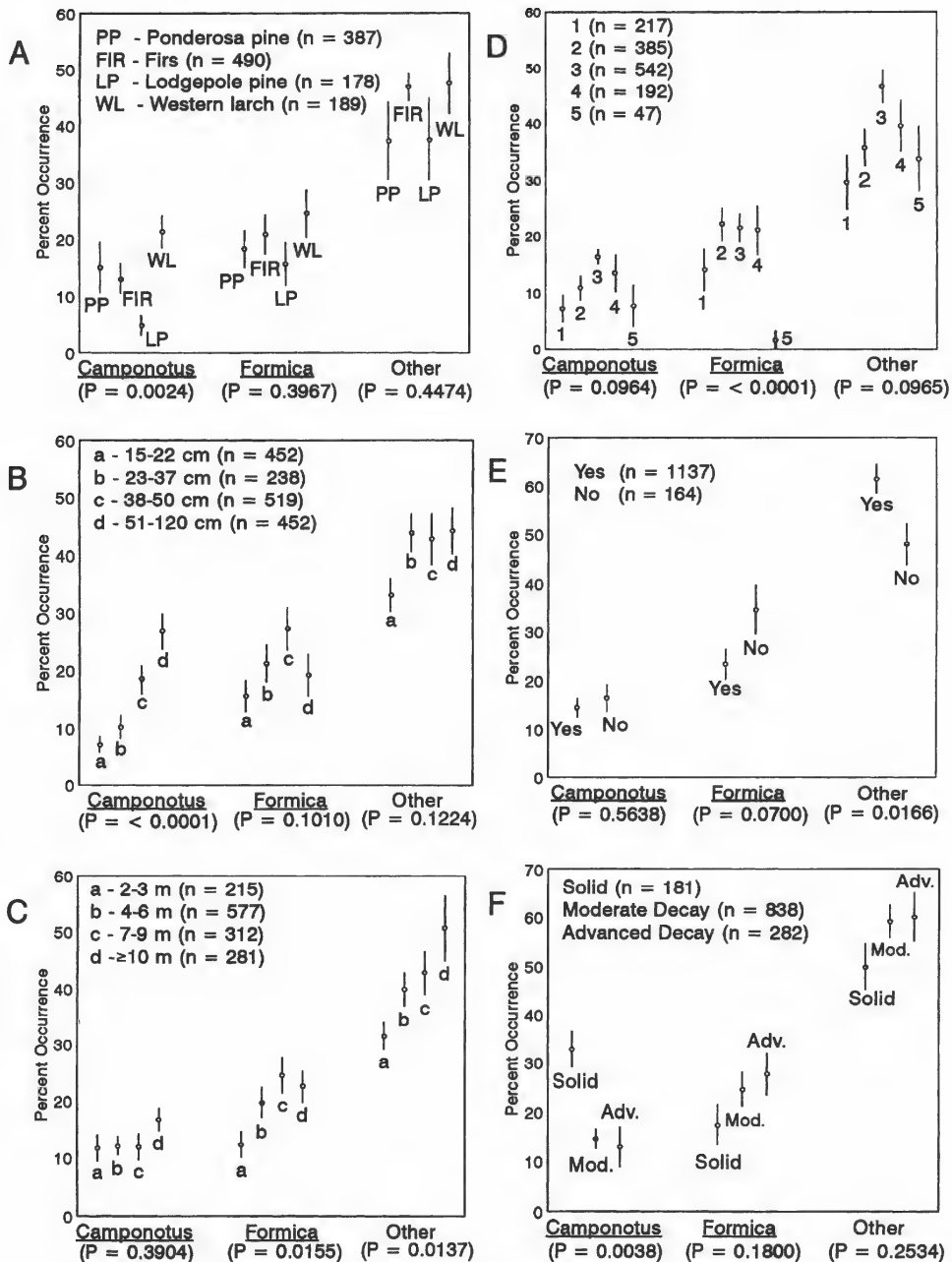


Figure 3. Percent occurrence of ants among logs classified by (A) tree species, (B) large-end diameter, (C) length, (D) log-decomposition, (E) ground contact, and (F) wood condition at sectioning cuts, in northeastern Oregon, May-July, 1991.

analysis indicated that the dominant variables for *Camponotus*, in the order entered, were large-end diameter (+), larch (+), log-decomposition class 3 (+), log-decomposition class 5 (-), and lodgepole pine (-). For *Formica* the dominant variables, in their order, were log-length (+), ground contact (-), log-decomposition class 5 (-), large-end diameter (+), and log-decomposition class 2 (+).

Discussion

Down wood is an important structural component for colonies of log-dwelling ants, as well as a foraging substrate for pileated woodpeckers looking for those ants. In addition, some of the ants are important because they are predators of larval western spruce budworm, a potentially damaging defoliating insect. The logs are the substrate that links these functional systems.

Logs of larch were the most significant colony substrate for the *Camponotus* ants, which showed an apparent aversion for lodgepole pine. Because larch logs averaged among the largest diameter logs, and lodgepole pine logs were the smallest, we were at first unsure whether species or diameter was the more significant variable. Discriminant analysis revealed that large-end diameter of logs was the dominant driving variable relating to occurrence of *Camponotus*. These ants used the largest diameter class of logs (51-120 cm) more than logs in the smallest diameter class (15-22 cm). The same analysis indicated that lodgepole pine logs were avoided even if they were of large diameter. The firs were used by *Camponotus* in about the same proportions (35.8%) in which they occurred among the sectioned logs (32.4%)(Table 1).

Significantly, Bull and Holthausen (1993), who sampled the same logs as used in this study, determined that pileated woodpeckers concentrated their foraging on larch and Douglas-fir and mostly avoided lodgepole pine. The birds also foraged more in logs with large-end diameters >37 cm—that is, in our two largest diameter classes (38-50 and 51-120 cm). Neither *Formica* nor the Other species showed significant differences in the proportions in which they occurred among species of logs or large-end diameter classes. Given that *Camponotus* is the preferred ant prey of pileated woodpecker (Bull et al. 1992), it is not surprising that the woodpeckers concentrated their forag-

ing on logs that were most likely to yield *Camponotus* ants.

Discriminant analysis revealed that *Camponotus* favored logs that, outwardly, were in the middle log-decomposition class (class 3), and both *Camponotus* and *Formica* tended to avoid the most decomposed logs (class 5). Contact of the log with the ground was a significant negative variable for *Formica*, which is consistent with their apparent aversion for the most decayed logs (log-decomposition class 5). Wood condition (i.e., the log's internal consistency) at the site of the sectioning cuts influenced the occurrence of *Camponotus*, which distinctly preferred more solid wood (Figure 3F). *Camponotus* and *Formica* tended to avoid the most outwardly decomposed logs with advanced internal deterioration, where presumably they would be most vulnerable to predation by a large, powerful excavator such as the pileated woodpecker. Overall, *Camponotus* and *Formica* tended to favor less decayed, large-diameter logs of larch or fir where they are most secure from predation by pileated woodpecker.

Of the nine identifiable species of *Camponotus* and *Formica* found in the sectioned logs (Table 3), six are documented predators of western spruce budworm in the montane West—*C. modoc*, *C. vicinus*, *C. laevigatus*, *F. neorufibarbis*, *F. accreta*, and *F. lasioides* (Youngs and Campbell 1984). Another species, *F. subnuda*, is a suspected predator.¹ The three species of *Formica* that are not documented predators of the budworm—*F. haemorrhoidalis*, *F. densiventris*, and *F. subnuda*—represented only 2.8% of the occurrences of ants and occurred in only 1% of all the logs. *Camponotus modoc*, the most common of the *Camponotus* we found, may emerge as the target prey species for the woodpecker in northeastern Oregon. Bent (1964) cites a record of pileated woodpecker stomach contents containing *C. herculeanus modoc* (= *C. modoc*, Smith 1979) obtained from two specimens of *Ceophloeus pileatus picinus* Bangs (= *D. pileatus*) in Yosemite Park, Calif. Bull et al. (1992) were not able to identify the *Camponotus* species in scat samples because identifying characters on the ants had been obliterated by passage through the gut of the woodpeckers.

A single species, rarely two, of documented budworm-foraging ants were found in 31.8% of the sectioned logs. Assuming that each log

represented a single colony of ants, there would be about 92 colonies of budworm-foraging ants among the 289.5 logs per ha. The volume of $110.8 \pm 3.24 \text{ m}^3$ per ha of downed woody material in our plots (Table 2) falls within the range of volume estimates ($115.9 \pm 3.5 \text{ m}^3$ per ha) for the mixed-conifer vegetation types predicted by Maxwell and Ward (1980). The volumes calculated for our study plots did not include logs with large-end diameters $<15 \text{ cm}$, whereas the comparable volumes from Maxwell and Ward (1980) included diameters down to 7.9 cm . Thus, even without the volume that would have been contributed by diameters between 7.9 and 14.9 cm , volumes in our pileated woodpecker home ranges were higher than the average of volumes observed by Maxwell and Ward (1980). This suggests that in mixed-conifer stands the upper levels of size classes 2, 3, and 4 of Maxwell and Ward (1980) approximate the tonnage of down wood needed to provide adequate foraging habitat in home ranges of pileated woodpecker.

The differential choice of down logs by each group of ants suggests a complex picture of the use of various species of logs of different sizes and in differing stages of decomposition. The possible temporal succession of particular groups of ants in different age classes of log decay may be a necessary function in the decomposition of down woody debris. This study and that of Bull and Holthausen (1993) together form a more com-

plete picture of how the pileated woodpecker and its prey base are related to down woody debris in the mixed-conifer stands of northeastern Oregon. Logging or firewood cutting practices that leave inadequate or unsuitable down-wood substrates for log-dwelling ants could affect populations of pileated woodpeckers.

Practices that result in inadequate amounts and kinds of down wood could affect pileated woodpecker populations and the beneficial role that foliage-foraging ants have in maintaining forest health. The relationships among ants, pileated woodpecker, forest-defoliating insects, and down logs illustrate the complex of interconnecting life-systems that form a functional ecosystem. Resource managers need to consider this diversity in developing guidelines that prescribe size, species, and amounts of large woody debris in order to conserve functional processes that foster sustainable forest ecosystems.

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Literature Cited

- Beckwith, R. C., and E. L. Bull. 1985. Scat analysis of the arthropod component of pileated woodpecker diet. *The Murrelet* 66:90-92.
- Bent, A. C. 1964. Life histories of North American woodpeckers. Smithsonian Institution, US National Museum Bull. 174. *In* Life Histories of North American Woodpeckers. Dover Publications, New York. Pp. 181-184.
- Brookes, M. H., R. W. Campbell, J. J. Colbert, R. G. Mitchell, and R. W. Stark. 1987. Western spruce budworm. USDA Forest Service—Coop. State Research Serv., Tech. Bull. 1694. Washington, DC. 198 p.
- Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. *J. Wildl. Manage.* 57:335-345.
- Bull, E. L., and C. Meslow. 1977. Habitat requirements of the pileated woodpeckers in northeastern Oregon. *J. For.* 75:335-337.
- Bull, E. L., R. C. Beckwith, and R. S. Holthausen. 1992. Arthropod diet of pileated woodpeckers in northeastern Oregon. *Northw. Nat.* 73:42-45.
- Campbell, R. W., and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. *Environ. Entomol.* 11:111-114.
- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous ants in the population dynamics of the western spruce budworm. *For. Sci.* 29:779-790.
- Hall, F. C., and J. W. Thomas. 1984. Silvicultural options. *In* Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington. Pp. 128-147. J. W. Thomas ed. USDA For. Serv., Agr. Handb. 553. 512 p.
- Hansen, L. D., and R. D. Akre. 1985. Biology of carpenter ants in Washington State (Hymenoptera:Formicidae:Camponotus). *Melandieria* 43:1-5.
- Holldobler, B., and E. O. Wilson. 1990. *The Ants*. The Belknap Press of Harvard Univ. Press, Cambridge, Mass. 732 p.
- Maser, C., R. G. Anderson, K. Cromack, Jr., J. Williams, and R. E. Martin. 1979. Dead and down woody material. *In* Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington. Pp. 78-90. J. W. Thomas ed. USDA For. Serv., Agr. Handb. 553. 512 p.

- Maser, C., and J. M. Trappe. 1984. The seen and unseen world of the fallen tree. USDA For. Serv., Gen. Tech. Rep. PNW-164. 56 p.
- Maxwell, W. G., and F. R. Ward. 1980. Photo series for quantifying natural forest residues in common vegetation types of the Pacific Northwest. USDA For. Serv., Gen. Tech. Rep. PNW 105. 229 p.
- Miller, R. G. 1981. Simultaneous statistical inference. Springer-Verlag. Pp. 37-48.
- Petal, J. 1978. The role of ants in ecosystems. Pp. 293-325. *In* Production ecology of ants and termites. M. C. Brain ed. Cambridge University Press, Cambridge. 408 p.
- SAS. 1988. SAS/STAT User's guide. Release 6.03 edition. SAS Institute Inc., Cary, North Carolina. 1029 p.
- Smith, D. R. 1979. Superfamily Formicoidea. *In* Catalog of hymenoptera in America north of Mexico. Vol. 2. Apocrita. eds. K. V. Krombein, P. D. Hurd, D. R. Smith, and B. D. Burks. Smithsonian Institution Press, Washington DC. Pp. 1323-1467.
- Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. 7th Ed. Iowa State Univ. Press, Ames.
- Torgersen, T. R., R. R. Mason, and R. W. Campbell. 1990. Predation by birds and ants on two forest insect pests in the Pacific Northwest. *In* Avian foraging: theory, methodology, and applications. eds. M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. Studies in avian biology 13:14-19. Cooper Ornith. Soc., Allen Press, Lawrence, Kansas.
- U.S. Laws, Statutes, etc. 1976. Public Law 94-588 {S. 3091}, Oct. 22, 1976 National Forest Management Act of 1976. *In* United States code congressional and administrative news. 94th Congress, 2nd Session, 1976. Vol. 2, Pp. 2949-2963. West Publ. Co., St. Paul, Minn. [1976.] [16 U.S.C. sec. 1600 1976].
- USDA Forest Service. 1985. Field procedures. Stand examination. Pacific Northwest Region. 62 p., appendices A-O.
- Way, M. J., and K. C. Khoo. 1992. Role of ants in pest management. *Ann. Rev. Entomol.* 37:479-503.
- Wheeler, G. C., and J. N. Wheeler. 1986. The ants of Nevada. Natural History Museum of Los Angeles County. Allen Press, Lawrence, Kansas. 138 p.
- Youngs, L. C. 1983. Predaceous ants in biological control of insect pests of North American Forests. *Bull. Entomol. Soc. Amer.* 29:47-50.
- Youngs, L. C., and R. W. Campbell. 1984. Ants preying on pupae of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in eastern Oregon and western Montana. *Can. Entomol.* 116:1665-1669.

Note

¹ Markin, G.P. From a paper, "Ants as predators of western spruce budworm." Presented at the Annual Meeting of the Entomological Society of America, Denver, Colorado. November 25-29, 1979. On file, Forestry and Range Sciences Laboratory, La Grande, Oregon. 97850, USA.

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Habitat Use by Juvenile Bull Trout in Belt-Series Geology Watersheds of Northern Idaho

Abstract

Bull trout (*Salvelinus confluentus*), a native char of the Pacific Northwest, has declined in abundance and distribution in recent years. Little is known about the habitat use by salmonids in streams with substrate characterized by Belt-Series geology. Such information could be used by managers to evaluate potential effects of land use practices on the species, or to enhance or protect existing habitat. A total of 28 pools, 60 riffles, and 46 runs was sampled in 14 reaches of four streams to determine habitat use of age 0 and age ≥ 1 juvenile bull trout in three habitat types (pools, runs, and riffles) and in channel margins and main channels. Age 0 bull trout used habitat types in equal proportion to availability, whereas age ≥ 1 juvenile bull trout selected pools and avoided riffles. Lateral position within the stream channel differed with age class: 88% of the age 0 fish were in the channel margins, whereas 91% of the age ≥ 1 fish were in the main channel. In addition to the habitat use study, 18 reaches in six streams were studied to determine habitat characteristics that influence abundance and distribution of juvenile bull trout. Reaches with high densities (3.9 to 11.2 fish/100 m²) of bull trout had maximum summer temperatures ranging from 7.8 to 13.9°C, whereas most reaches with low densities (< 1.0 fish/100 m²) had higher maximum summer temperatures (18.3 to 23.3°C). Density of juveniles in reaches increased with the number of pocket pools/100 m. The combination of number of pocket pools and maximum summer temperature explained nearly two-thirds of the variation in density of juvenile bull trout.

Introduction

The bull trout (*Salvelinus confluentus*), a native char of the Pacific Northwest, has declined in abundance and distribution during the past 30 years (Goetz 1989), especially in southern portions of its range (Rode 1988). Several factors have been implicated in their decline, including habitat degradation (Cardinal 1980; Enk 1985), competition with introduced species (Dambacher et al. 1992), and exploitation (Allan 1980; Carl 1985). Bull trout gained their southern distributions during the Miocene and Pleistocene epochs when major river systems of the Northwest were connected and the climate cooler (Goetz 1989). As temperatures warmed, bull trout took refuge in cold headwater streams. Some populations of bull trout are year-round stream residents, whereas others are migratory, requiring downstream passage from natal streams to a river or lake to grow to maturity and upstream passage to return for spawning. McPhail and Murray (1979) suggested that lack of rearing habitat may limit the overall number of bull trout in a population. However, compared

to most other salmonids, little is known about the specific rearing requirements of bull trout.

When evaluating the habitat requirements of bull trout, the geology of watersheds should be considered. Much of northern Idaho and northwestern Montana consists of Belt-Series geology characterized by cobble-sized sediments. Little is known about the habitat use by salmonids in streams with Belt-Series type substrate. Such information could be used by managers to evaluate potential effects of land use practices on the species, or to enhance or protect existing habitat. The objectives of this study were to 1) characterize habitat use of age 0 and older juvenile bull trout in summer and 2) identify the physical attributes of streams that are most closely associated with the distribution and abundance of bull trout. Although habitat for juvenile bull trout can be limiting in any season (e.g., winter), the emphasis in this study was on late spring and summer, when conditions for growth of juveniles were most favorable.

Study Area

The study was conducted in 18 reaches of six different tributary streams (Grouse Creek, North Fork

¹ Current address: Shoshone-Bannock Tribes, Fisheries Department, Fort Hall, Idaho 83203

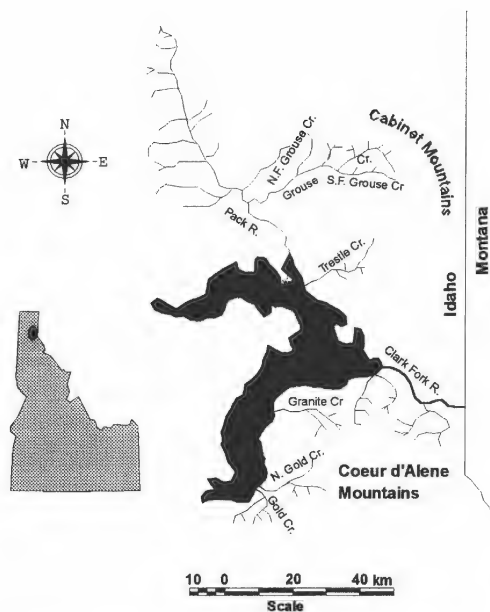


Figure 1. Map of study area including geographic location of Lake Pend Oreille, its major tributaries, and the study streams.

Grouse Creek, Trestle Creek, Granite Creek, North Gold Creek, and Gold Creek) of the Lake Pend Oreille drainage in northern Idaho (Figure 1). In these and other Lake Pend Oreille tributaries, juvenile bull trout most often occur sympatrically with resident and juvenile adfluvial westslope cutthroat trout (*Oncorhynchus clarki lewisi*), resident and juvenile adfluvial rainbow trout (*O. mykiss*), and occasionally with brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) (Pratt 1985). Most bull trout in these systems are adfluvial, typically remaining in streams as juveniles from one to three years, and migrating to the lake to grow (often up to 65.0 cm in length) and mature (Hoelscher and Bjornn 1989). Maturity occurs within two to four years after reaching the lake, so adult fish are typically five to seven years old. Adult bull trout have strong homing instincts (Scott and Crossman 1973), returning to their natal streams during spring through early fall and spawning during September and October.

Streams were chosen to represent the range of habitats accessible to and occupied by adfluvial bull trout in the Belt-Series geology type rock formation located on the eastern side of Lake Pend

Oreille (Figure 1; Table 1). Details of the study streams are presented in Saffel (1994). Eighteen stream reaches to be sampled were systematically placed within the stream distance available to adfluvial bull trout. Length of study reaches was approximately 100 m in thalweg length. However, one reach at the lower end of Granite Creek was divided into two, smaller reaches because a large spring in the middle of the original reach reduced the water temperature by 5°C.

Methods

Density of Juvenile Bull Trout

Numbers of juvenile bull trout were estimated within each study reach by snorkeling and bank observation at night between 6 July and 4 September 1992. Night snorkeling was shown to be a consistently better method of enumerating juvenile bull trout than day snorkeling or electrofishing in three Lake Pend Oreille tributaries (Bonneau 1994). Snorkel counts were made by moving upstream through the reach, spotting fish with a flashlight, and whenever possible, confirming the length with an object of known length. A bank observer followed approximately 15 m behind the snorkeler and counted fish in the channel margins on both banks. To avoid duplicate counting of fish, the bank observer and snorkeler communicated and used hand signals to indicate fish locations and counts. Bull trout would remain motionless when observed with a light from underwater and from above, facilitating identification and length estimation. Bull trout were categorized according to total length as: Age 0 (< 75 mm) and age ≥ 1 (75 to 270 mm). Fish were later consolidated into one group, juvenile bull trout (age 0 and age ≥ 1 combined), for analysis of abundance and distribution. Length at age categories were confirmed by a small sample of otoliths collected from study streams. Length of age 0 fish was typically 40 to 60 mm with the largest being 75 mm. Counts of fish were recorded according to observation method (snorkeling or from the bank), species, and size class. Age 0 bull trout were distinguished from other age 0 salmonids by an overall darker, mottled body color, the absence of markings on dorsal fin, a laterally compressed body form, and the presence of a black, triangular-shaped mark on the caudal fin. Hybrid bull trout x brook trout were differentiated from bull trout by spotting on the dorsal fin (Cavender

TABLE 1. Key physical, chemical, and biological attributes of the six study streams. Geologic types are, UGB, unglaciated belt; GB, glaciated belt; and GM, granitic mix. Other trout species are: ctt, cutthroat trout; rbt, rainbow trout; brt, brook trout; and hyb, brook trout x bull trout hybrids. Discharge was measured on 27 and 28 August.

Creek	Geologic type	August discharge (m ³ /s)	Conductivity μ mhos cm ⁻¹	Percent gravel ^a	Range of gradient (%) ^b	Elevation lower-upper (m) ^c	Other trout species observed
Gold	UGB	0.23	99	47.1	3.8	628 - 725	ctt
North Gold	UGB	0.11	107	49.6	6.4	628 - 670	ctt
Granite	UGB	0.23	88	36.2	1.9 - 5.4	628 - 805	ctt, rbt
Trestle	GB	0.21	34	30.0	3.1 - 8.3	628 - 1,158	ctt, rbt
Grouse	GM	0.21	17	13.5	1.6 - 3.6	902 - 1,228	ctt, rbt, hyb
N.F. Grouse	GM	0.05	90	35.2	3.5-5.0	750 - 878	rbt, brt, hyb

^a Dominant gravel substrate includes both pea gravel and gravel (Overton 1992). This size range corresponds with dominant substrates characterizing bull trout redds (Goetz 1989).

^b Gradients are those reported by Hoelscher and Bjornn (1989) that corresponded with sections in this study and are approximations.

^c Elevations are approximations as reported by Hoelscher and Bjornn (1989).

1978; Markle 1992). Densities (fish/100 m²) were calculated based on the dimensions of each reach in which fish were counted.

Temperature

Water temperature in the 18 study reaches was monitored with 14 maximum-minimum thermometers and four Ryan Tempmentors. A thermometer or Tempmentor was placed directly below each study reach by 18 June and removed on 10 and 11 September. Maximum-minimum thermometers were read every two weeks. Tempmentors recorded hourly temperatures. Temperatures throughout study reaches were confirmed with a hand-held thermometer at times of snorkeling. Maximum summer temperature was chosen for analysis because it has been cited as a controller of juvenile bull trout distribution (Goetz 1989) and is commonly used in relating fish abundance to habitat.

Use of Habitat Types

To determine use of habitat types, twenty-eight pools, 60 riffles, and 46 runs were sampled from 14 reaches in four streams during July and August of 1992. Habitat typing followed the procedure described by Overton (1992). This procedure used information from Bisson et al. (1981) and Sullivan (1986) to determine habitat types.

To determine physical features of the pools, riffles, and runs, three equidistant transects parallel

and perpendicular to flow were placed in each habitat unit. As a result, nine points within each habitat unit were measured for water depth, bottom water velocity (2 cm above bottom), and dominant substrate. Depth was measured with a meter stick, velocity with a Marsh-McBirney flow meter, and dominant substrate was estimated visually within a 0.3 m² area around each point. Length was measured along the thalweg, wetted stream width was measured at each perpendicular transect, and bankfull channel width was measured at each one-half transect.

Mean depth, geometric mean substrate size, and mean velocity was determined for each habitat unit. Mean depth (cm) of habitat units was calculated as the sum of the nine depths divided by 12 to account for 0 depth at the bank (Platts et al. 1983). Geometric mean substrate size was determined using ranked classifications described by Overton (1992): sand/silt (< 0.2 cm; rank = 1), pea gravel (0.2 - 0.6 cm; rank = 2), gravel (0.6 - 7.5 cm; rank = 3), rubble (7.5 - 15.0 cm; rank = 4), cobble (15.0 - 30.0 cm; rank = 5), boulder (> 30 cm; rank = 6), and bedrock (rank = 7). Mean velocity was equal to the sum of velocity measurements in a habitat unit divided by nine.

Reaches

To determine habitat features of reaches most closely associated with abundance and distribution of bull trout, six habitat variables were

measured for each study reach. Mean depth, mean velocity, and substrate diversity were calculated from transect measurements in habitat units. Other measurements included volume of large woody debris (volume/100 m²) within bankfull width, water temperature, and number of pocket pools.

Mean depth and mean velocity in a reach were calculated from data collected for habitat units. Diversity of substrate was estimated using the reciprocal of Simpson's index (Hill 1973), $D=1/\sum (P_i^2)$; where, P_i is the proportion of substrate measurements in category i .

Volume of large woody debris within bankfull discharge was estimated for each reach. Pieces measured were defined as either a bole or rootwad. Boles were greater than 10 cm in diameter at one-third the distance from the base and either (1) equal to or longer than 3 m in length or (2) two-thirds the stream width (Overton 1992). Root wads were attached to logs less than three meters in length. Diameter was measured at one meter from the base. The volume was estimated using the formula for determining the volume of a cylinder; $\pi(r^2)l$; where, r = the radius at one-third (bole) or one meter (root wad) the distance up from the base and l = the length.

The total number of pocket pools was determined for each study reach. Pocket pools were small, low velocity areas formed by channel obstructions including boulders, woody debris, and irregular bank formation (Overton 1992). Pocket pools were characterized by less turbulence, smaller substrate, and generally greater depth than surrounding areas and were in riffle and run habitat types.

Analyses

Chi-square contingency tables and goodness-of-fit tests were used to determine whether use of habitat types by bull trout was independent of age class (age 0 and age ≥ 1). Use was determined by pooling habitat unit counts from Granite Creek, Trestle Creek, North Gold Creek, and Gold Creek. Reaches 1 and 2 from both Grouse and North Fork Grouse creeks were excluded because factors other than physical habitat features (i.e., high temperatures and presence of brook trout) may have limited bull trout numbers there. Observed values by age class were equal to the number of fish counted in a habitat type. Expected values were

calculated based on the proportion of area sampled of a habitat type. The null hypothesis was that use of habitat type was in proportion to the availability of a particular habitat type. If use of habitat types by an age class was significantly different (i.e., $P \leq 0.05$), Bonferroni confidence intervals around frequency of use were used to determine if bull trout age classes were selecting, neutral, or avoiding habitat types (Neu et al. 1974). Selection for a habitat type was indicated if availability of a habitat type was lower than the lower bound of the confidence interval. Conversely, avoidance was indicated when availability of a habitat type was higher than the upper bound. Neutral selection was indicated when the frequency of the habitat type was within the bounds of the confidence interval.

To test for differences in mean velocity, mean depth, and geometric mean dominant substrate size between habitat types, the Kruskal-Wallis test was used because of unequal variances and non-normal distributions of samples. Dunn's test was used for multiple comparisons of ranked values with unequal sample size. Each test was considered significant at $P \leq 0.05$.

Regression techniques were used to relate bull trout densities to the six habitat variables (volume of large woody debris/100 m², mean depth, substrate diversity, maximum summer temperature, mean velocity, and number of pocket pools/100 m). Multiple best subsets regression, with Mallows' C(p) statistic as a criterion, was used to choose the five best models with two independent variables. For multiple and simple linear regression tests, density of juvenile bull trout was the dependent variable (Y) and habitat features were the independent variables (X). Multiple and simple linear regression results were considered significant at $P \leq 0.05$.

Normality and homoscedasticity assumptions were evaluated to determine the validity of regression analyses and the need for transformations. Transformations of density of juvenile bull trout and volume of large woody debris were necessary to normalize distributions and stabilize variance. Density of bull trout was transformed using a square root ($Y + 0.5$) transformation and volume of large woody debris was transformed using $\log_{10}$. For regression procedures the constant variance assumption was visually determined using residual plots (Zar 1984).

Results

Use of Habitat Types

A total of 190 age 0 and 253 age ≥ 1 juvenile bull trout was observed during July and August in 14 reaches of four streams (Table 2). Use of habitat types was dependent on age (size) of bull trout ($\chi^2 = 28.26$; 2 df; $P < 0.001$), so different age classes used habitat types differently. Age 0 bull trout showed no selection for a habitat type ($\chi^2 = 3.83$; 2 df; $P > 0.10$). Age ≥ 1 bull trout, in contrast, were found more often than expected in pools and less than expected in riffles ($\chi^2 = 24.43$; 2 df; $P < 0.001$). Use of channel margins and main channels by juvenile bull trout was also related to age class. Eighty-eight percent of the age 0 fish were observed in the channel margins, whereas 91% of the age ≥ 1 were found in the main channel.

For Granite, North Gold, Gold, and Trestle Creeks combined, riffle habitat was most abundant (3,793.5 m²) followed by runs (2,344.1 m²) and pools (962.5 m²). Significant differences were found between habitat types in mean velocity ($H = 51.7$; 2 df; $P < 0.001$; Figure 2), geometric mean substrate size ($H = 29.1$; 2 df; $P < 0.001$), and in mean depth ($H = 44.4$; 2 df; $P < 0.001$). Mean comparisons indicated similarities in mean depth and mean velocity between pools and runs, whereas

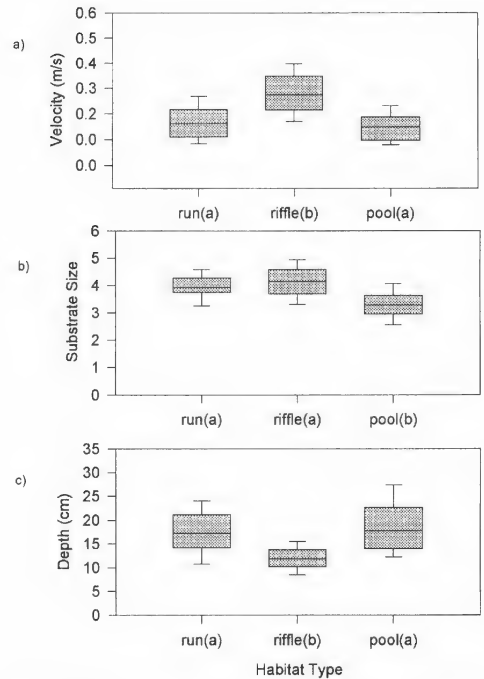


Figure 2. Box plots showing 10th, 25th, 50th, 75th, and 90th percentiles (horizontal lines) for a) mean velocity, b) geometric mean substrate size, and c) mean depth by habitat type (pool, riffle, and run) for four streams during July and August. Different small case letters next to habitat types indicates significant differences between those types. Dunn's test was used for multiple comparisons.

TABLE 2. Availability of three habitat types and use by juvenile bull trout in four streams during July and August 1992.

	Pool	Riffle	Run	Totals
n	28	60	46	134
Habitat area (m ²)	962.5	3,793.5	7,100.2	11,856.2
Available (%) ^a	13.6	53.4	33	
Age 0 bull trout				
n	17	111	62	190
Use (%)	9.0	58.4	32.6	
Age ≥ 1 bull trout				
n	61	115	77	253
Use (%)	24.1	45.5	30.4	
Confidence interval	17.7 - 30.6 ^b	37.9 - 53.0 ^c	23.5 - 37.4	

^a Percent of total habitat area

^b Selection for pool habitat

^c Avoidance of riffle habitat

riffles were shallower and had higher velocities. Substrate size was significantly larger in both runs and riffles than in pools. Therefore, in combination with the habitat use results, it can be concluded that age ≥ 1 juvenile bull trout were found more often than expected in deeper, slower habitat types with smaller substrate (i.e., pools). Conversely, age ≥ 1 juvenile bull trout were observed less often than expected in shallower, faster habitat types with larger substrate (i.e., riffles).

Reaches

Juvenile bull trout were found at elevations ranging from 628 m to 1158 m and gradients ranging from 1.9% to 8.3% (Table 1). Densities of juvenile bull trout (age 0 and age ≥ 1 combined) ranged from zero to 11.2/100 m² (Table 3). Two variables, maximum summer temperature and number of pocket pools/100 m, were significantly related with density of juvenile bull trout using simple linear regression. None of the other four habitat variables (mean depth, mean velocity, substrate di-

versity, or log₁₀ volume of large woody debris) was significantly related to density of bull trout.

The density of juvenile bull trout was negatively related with maximum summer temperature ($r^2 = 0.33$; $df = 17$; $P = 0.01$). However, a non-linear, dome shaped relationship or barrier effect (temperatures are either too low or high to support the species) is more likely (Figure 3). Density of bull trout increased with increasing temperature below 14°C and decreased with increasing temperature above 18°C. The highest densities of bull trout were found in Trestle and Gold Creeks where maximum summer temperatures ranged from 10 to 13.9°C. Lower densities of bull trout were found with decreasing maximum summer temperatures below 13.9°C in North Gold Creek and portions of Granite Creek and with maximum summer temperatures above 18°C in the Grouse Creek drainage and in one reach of Granite Creek. No reaches were sampled that had maximum summer temperatures between 14 and 18°C. This may be due to the relatively warm

TABLE 3. Physical characteristics and densities of juvenile bull trout in 18 stream reaches of six Lake Pend Oreille tributaries.

Creek	Reach	Length (m)	Mean width (m)	Mean depth (cm)	Substrate diversity	Mean velocity (m/s)	Volume of large woody debris/100 m ²	Maximum summer temperature (°C)	Number of pocket pools/100 m	Juvenile bull trout/ 100 m ²
Granite	1	43.6	6.38	14.93	2.96	0.20	1.92	12.2	6.88	5.39
Granite	2	64.9	6.19	16.34	1.92	0.11	0.96	18.3	0	0.75
Granite	3	105.8	5.55	15.49	3.02	0.21	2.24	13.9	0	0.85
Granite	4	111.8	5.13	15.10	4.25	0.18	2.44	11.0	14.31	4.01
Granite	5	92.4	5.92	16.82	3.24	0.20	2.12	9.2	20.56	4.94
Grouse	1	89.0	7.37	13.52	3.11	0.17	0.80	20.0	20.22	0.30
Grouse	2	83.0	6.25	10.39	3.67	0.12	0.20	20.0	28.92	0.96
N.F. Grouse	1	88.7	4.76	10.12	3.61	0.30	2.44	23.3	6.76	0.00
N.F. Grouse	2	90.1	4.92	10.88	4.56	0.25	3.12	20.0	6.66	0.23
North Gold	1	95.7	5.01	12.57	2.45	0.12	9.84	7.8	0	0.42
North Gold	2	100.9	4.85	14.93	3.73	0.18	6.92	7.8	6.94	3.88
Gold	1	108.6	6.65	11.92	3.59	0.22	0.48	10.0	21.18	7.89
Gold	2	89.3	3.90	15.63	2.90	0.23	3.12	11.1	24.64	11.20
Trestle	1	103.6	6.57	17.06	3.73	0.17	2.40	13.0	25.10	8.96
Trestle	2	128.6	5.05	13.20	4.00	0.23	4.92	13.3	30.33	7.55
Trestle	3	123.6	5.22	16.22	3.90	0.24	4.88	13.9	20.23	11.16
Trestle	4	101.5	4.43	11.72	3.49	0.20	6.08	12.2	12.81	6.23
Trestle	5	105.3	4.16	8.23	3.71	0.18	16.28	12.1	17.09	9.82

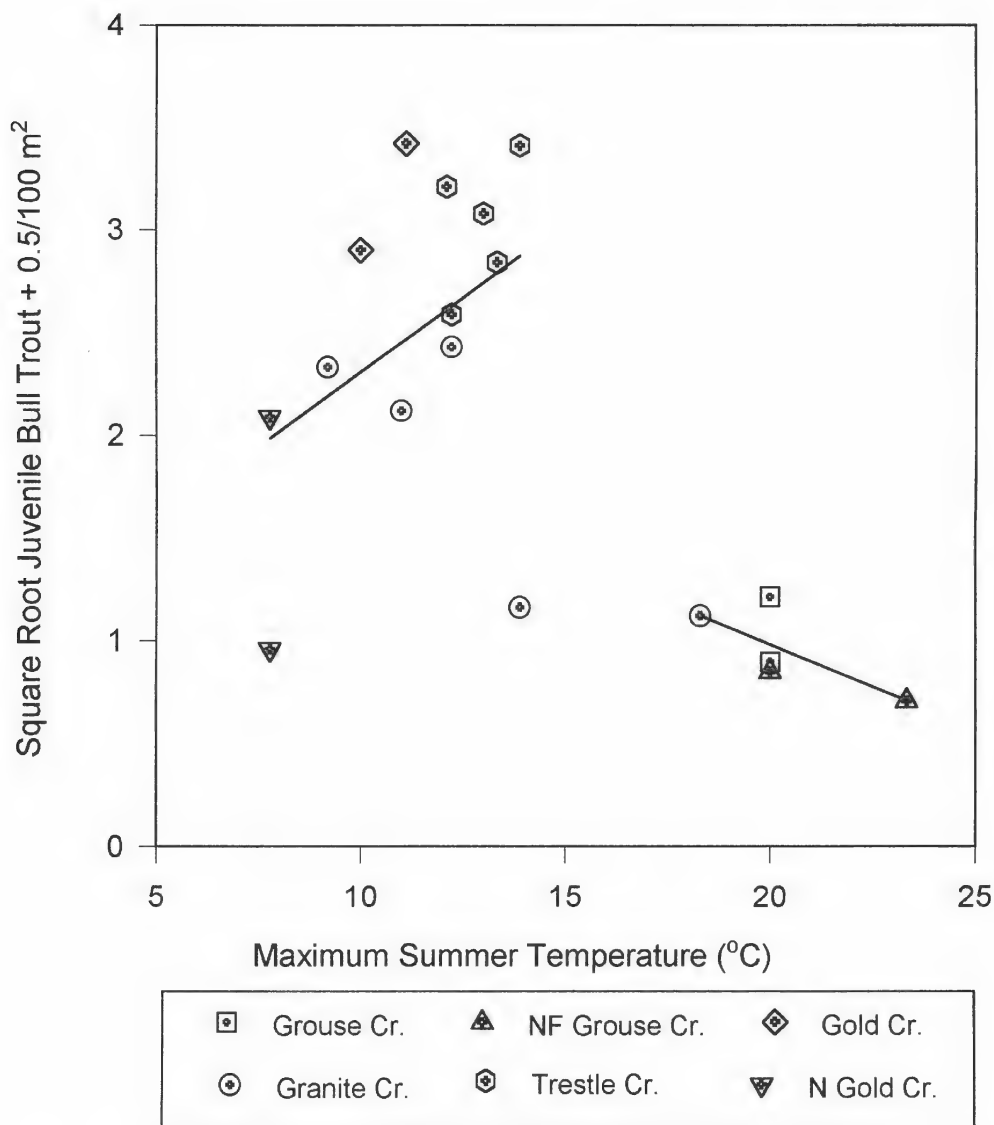


Figure 3. Scatter plot of maximum summer temperature and transformed juvenile bull trout density for 18 reaches of six streams. Lines indicate trends in density of juvenile bull trout in reaches with maximum summer temperatures $<14^{\circ}\text{C}$ (increasing trend) and $>18^{\circ}\text{C}$ (decreasing trend).

summer climate in the Lake Pend Oreille drainage. Low elevation (690 m at lake level) and consistently warm summer air temperatures (often above 30°C) may result in warm stream temperatures except where influence of cold ground water

is significant or the stream is shaded from sunlight.

The density of juvenile bull trout was positively related with number of pocket pools/100 m ($r^2 = 0.33$; $df = 17$; $P = 0.01$; Table 4; Figure

TABLE 4. Results of simple linear regression between density of juvenile bull trout (Y) and independent variables (X) for 18 reaches (df = 17) of six streams.

Independent Variable (X)	r ²	F	Probability	Equation
No. of pocket pools/100 m	0.33	7.87	0.01	Y = 1.26 + 0.06(X)
Mean bottom velocity	0.04	0.59	0.46	Y = 1.33 + 3.75(X)
Mean depth	0.06	1.01	0.33	Y = 0.84 + 0.09(X)
Substrate diversity	0.05	0.88	0.36	Y = 0.87 + 0.35(X)
Volume of large woody debris (log ₁₀)	0.09	1.6	0.22	Y = 1.63 + 1.65(X)

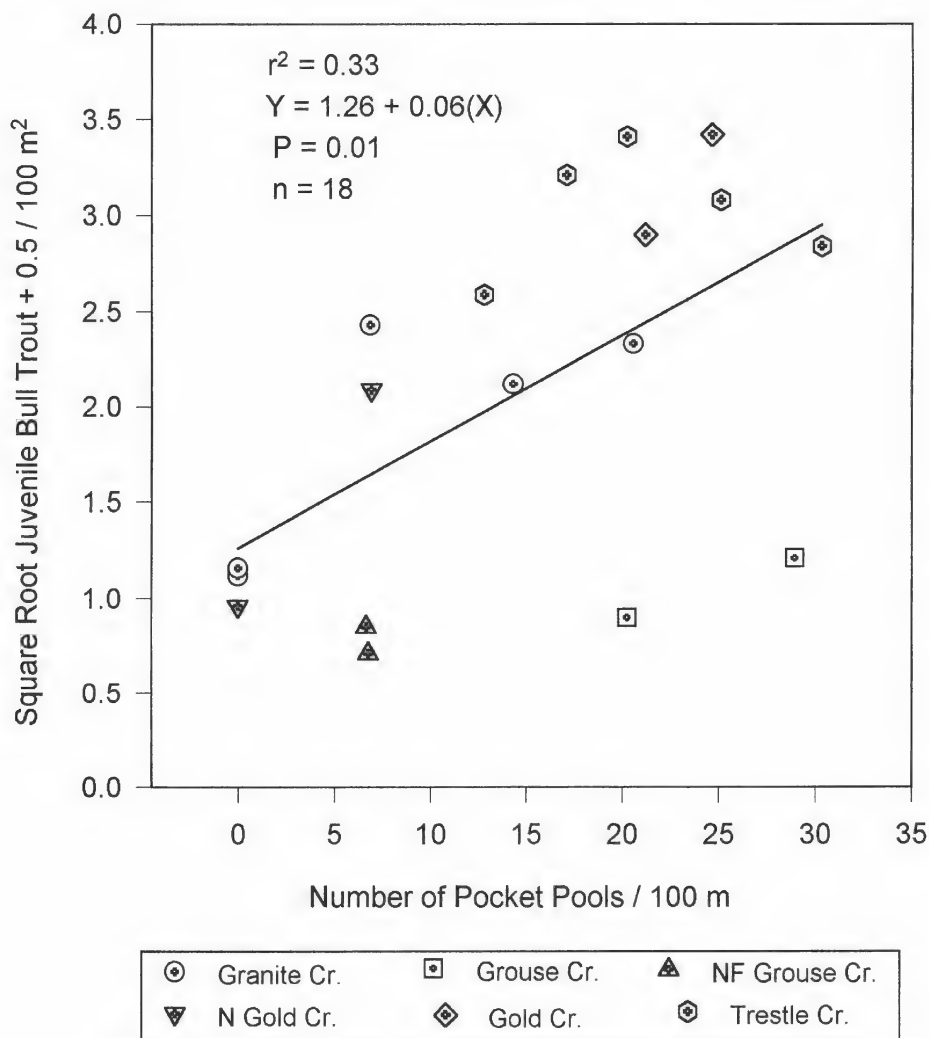


Figure 4. Relationship between number of pocket pools/100 m and transformed juvenile bull trout density for 18 reaches of six streams.

4). Density of juvenile bull trout in the four reaches within Grouse Creek and North Fork Grouse Creek was poorly described by the linear model and decreased the amount of variation explained (r^2). These four reaches differed from the others in that maximum summer temperatures were $> 18^\circ\text{C}$ whereas the other reaches had maximum summer temperatures of $< 14^\circ\text{C}$.

Using multiple best subsets linear regression, transformed juvenile bull trout density (Y) was best predicted by the model: $Y = 2.919 - 0.119(X_1) + 0.055(X_2)$ where X_1 = maximum summer temperature, and X_2 = number of pocket pools/100 m ($R^2 = 0.64$; $df = 16$; $P < 0.001$; Table 5; Figure 5). Number of pocket pools accounted for 33% of the variation and maximum summer temperature accounted for 31%. Colinearity between number of pocket pools and maximum summer temperature was insignificant ($r = -0.02$; $P > 0.90$). Model numbers 2 through 5 (Table 5) were also significant, however, in each case either maximum summer temperature or number of pocket pools were included in the model and accounted for most of the variation.

The interpretation of the temperature data in this study is limited because of the dependence of maximum summer temperature on streams (indicated by the clustering of individual reaches by stream in Figures 4 and 5) and by the absence of maximum summer temperature data between 14 and 18°C . Clustering of individual stream reaches is not unexpected because sections of streams accessible to bull trout were relatively short, resulting in little variation in water temperatures within a stream. An exception was Granite Creek, which consisted of cold stream temperatures (maximum summer temperatures of 9.2 and 11°C) at

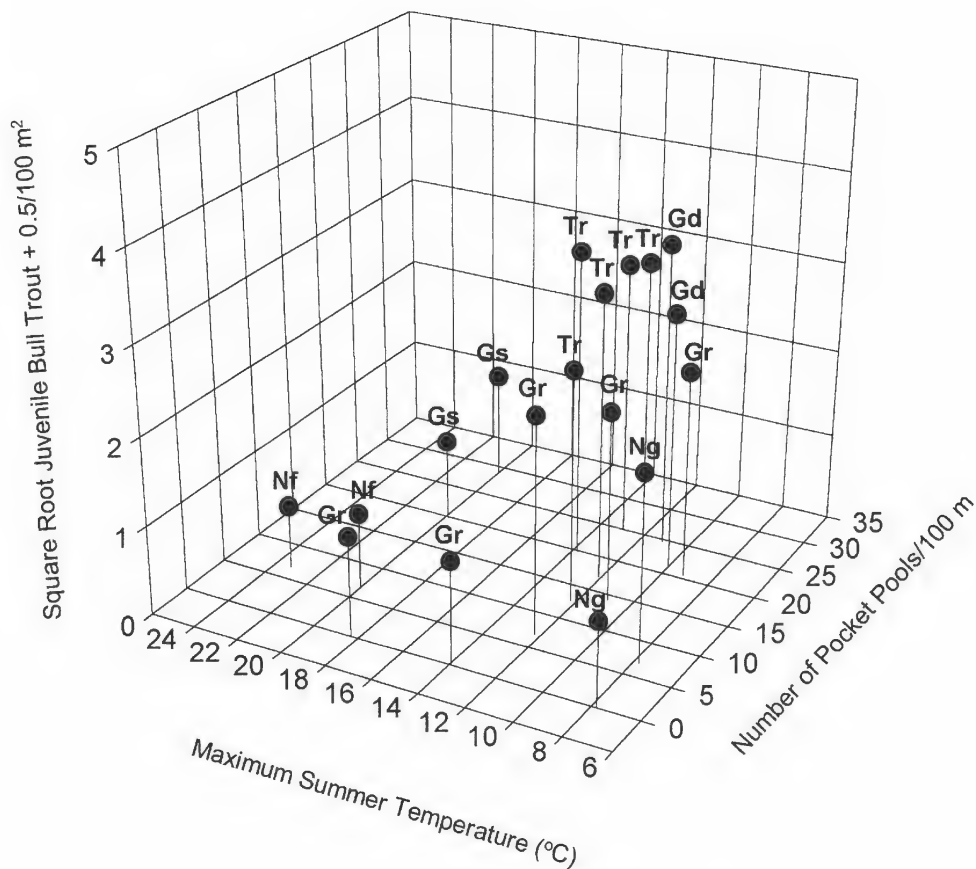
the upper reaches, warm stream temperatures (13.9 and 18.3°C) in the middle reaches, and low temperatures (12.2°C) at the lowermost reach, where the stream was influenced by a large, cold water spring. Densities of bull trout were highest in the upper and lowermost reaches where temperatures were coolest, and lowest in the middle two reaches.

Discussion

Age 0 bull trout used habitat differently than age ≥ 1 bull trout. Age 0 fish were found primarily in the channel margins of runs and riffles, whereas the older juveniles selected deeper, slower pool areas and exhibited an avoidance of riffles and runs. Segregation of habitat between larger, older salmonids and younger, smaller salmonids has been reported for bull trout in the upper Arrow Lakes drainage, British Columbia (McPhail and Murray 1979), for age 0 and older char (bull trout and brook trout) in Sun Creek, Oregon (Dambacher et al. 1992) and for steelhead trout (*O. mykiss*) and chinook salmon (*O. tshawytscha*) in two Idaho streams (Everest and Chapman 1972). Use of higher velocity, main channel areas for food acquisition requires stronger swimming, which may also exclude smaller fish. Channel margins often provide the necessary habitat for salmonid fry to survive. Moore and Gregory (1988) reported that age 0 cutthroat trout (*O. clarki*) were more abundant and had higher biomass in stream margins that provided slow, shallow water, and abundant food. Chapman and Bjornn (1969) and Everest and Chapman (1972) suggested that smaller steelhead trout fry used stream margins in the presence of chinook fry because of reduced predation by the larger chinook fry. In the present study, potential predators of age 0 bull trout included

TABLE 5. Results of multiple best subsets linear regression between transformed juvenile bull trout density (Y) and independent variables (X) for 18 reaches of six streams. Asterisks indicate use of independent variables in the respective models.

Model number	C(p)	R^2	Adjusted R^2	P	Maximum summer temp. ($^\circ\text{C}$)	Vol. of large woody debris/100 m^2	Substrate diversity	No. of pocket pools/100 m	Mean depth (cm)	Mean velocity (m/s)
1	4.33	0.64	0.59	0.0005	*			*		
2	11.23	0.49	0.42	0.0066		*		*		
3	14.35	0.42	0.34	0.0168	*					*
4	15.00	0.41	0.33	0.0202	*		*			
5	15.87	0.39	0.31	0.0256				*	*	



$$R^2 = 0.64$$

$$P < 0.001$$

$$Y = 2.919 - 0.119(X_1) + 0.055(X_2)$$

$$n = 18$$

Gd = Gold Creek
Gr = Granite Creek
Ng = North Gold Creek
Tr = Trestle Creek
Nf = North Fork Grouse Creek
Gs = Grouse Creek

Figure 5. Relationship between maximum summer temperature, number of pocket pools (independent variables) and transformed juvenile bull trout density for 18 reaches of six streams.

cutthroat trout, rainbow trout, brook trout, and larger bull trout. Bull trout greater than 110 mm have been found in other areas to prey upon other bull trout (Horner 1978; Shepard et al. 1984).

The density of juvenile bull trout increased with increased numbers of pocket pools. Pocket pools provided refuge from high current velocities as well as visual isolation among individual fish.

Positions of refuge, whether in pools or pocket pools, are preferred by salmonids because they offer access to food with little energy expenditure (Fausch 1984). Pratt (1984) and Shepard et al. (1984) reported that juvenile bull trout commonly use small pockets with low water velocities just above the stream bed. Visual isolation may be particularly important to juvenile bull trout

because they may demonstrate a fixed-site territoriality (Pratt 1984). Pratt (1985) suggested that densities of bull trout may be controlled by the availability of areas providing visual isolation and refuge from higher velocities. Unlike cutthroat trout, which are commonly found throughout the water column in pools, juvenile bull trout numbers may be limited in pools by their territorial, bottom dwelling behavior. Pocket pools may thus provide additional rearing space for juvenile bull trout when pool habitat is unavailable. Pool habitat was the least abundant habitat type in all streams except North Gold Creek, where it was the second most abundant (Table 6). Placement of large rocks in nursery streams has been shown to result in the increase in the number of juvenile chinook salmon (Bjornn 1971) and Atlantic salmon (Redmond 1975).

In this study, density of bull trout increased with increasing temperature at lower temperatures and decreased with increasing temperature at higher temperatures. Past investigators have suggested that the relationship of temperature to the distribution of bull trout and other char is a barrier effect (few, if any, fish existing above a certain temperature). In this study, high densities of juvenile bull trout were not present in stream reaches with maximum summer temperatures above 13.9°C. These results are consistent with those of Fraley and Shepard (1989), where a summer maximum temperature of 15°C limited distribution of juvenile bull trout in the Flathead Lake and River system, Montana. Jensen (1981) suggested that a maximum temperature of 14°C controlled the distribution of arctic char *Salvelinus alpinus*. The thermal barrier for brook trout has been reported to be a maximum temperature of 24°C (Ricker

1934; MacCrimmon and Campbell 1969; Meisner 1990). In this study, stream reaches with maximum summer temperatures below 13.9°C showed increasing density of bull trout with increasing temperature. Little is known about how temperature regulates density of fish in the wild. In laboratory channels, Hahn (1977) found a decreasing trend in steelhead trout density with increasing, yet suitable, temperature (opposite of the trend in this study). One plausible explanation is that the increasing trend in densities of bull trout between 7.8 and 13.9°C found in this study is influenced by increased growth and survival (mediated by the availability of food) in stream reaches with increasing maximum summer temperatures up to 13.9°C. The availability of food was not estimated in this study but may be one reason reaches are clustered by stream in Figures 4 and 5. More information is needed on the effect of temperature and availability of food on density of bull trout.

High water temperatures may be physiologically constraining on juvenile bull trout. Summer is the season in which maximum growth of fish would be expected; however, at temperatures above the preferred range for growth, increased metabolic processes may result in most or all food being used for maintenance. When Shepard et al. (1984) compared temperature and growth of juvenile bull trout in two tributaries of the Flathead River, Montana, they found that at warmer water temperatures, fish growth decreased despite higher primary productivity. In laboratory tests, bull trout fry grew largest and had the greatest survival at colder water temperatures with the greatest growth occurring at 4°C (McPhail and Murray 1979). The

TABLE 6. Area and percent of habitat types sampled in six streams during the summer of 1992.

Creek	Pool		Riffle		Run		Total Area (m ²)
	Percent	Area (m ²)	Percent	Area (m ²)	Percent	Area (m ²)	
Granite	11.3	263.57	53.8	1253.47	34.9	813.13	2330.17
Grouse	3.4	40.02	61.8	730.99	34.9	412.46	1183.47
NF Grouse	17.1	97.45	32.8	186.48	50.0	284.48	568.41
N Gold	27.0	293.55	51.5	559.55	21.5	233.8	1086.9
Gold	13.1	136.07	61.1	634.54	25.7	267.2	1037.75
Trestle	10.2	269.27	50.9	1345.94	38.9	1029.93	2645.14
Totals	12.4	1099.93	53.2	4710.97	34.4	3041.0	8851.84

lowest survival and growth was between 8 to 10°C. Most charrs are well adapted to cold water, and therefore it is plausible that the bull trout's preference would also be for cold water.

Water temperature may also be a decisive factor in influencing competitive advantage between bull trout and other coexisting species, such as brook trout and rainbow trout. Low bull trout densities and high temperatures were found in reaches of North Fork Grouse, Grouse Creek, and Granite Creek. Brook trout inhabited North Fork Grouse Creek and are likely competitors with juvenile bull trout for food and space (Wallis 1948; Dambacher et al. 1992). In addition, hybrids (bull trout x brook trout) were observed in both Grouse and North Fork Grouse Creeks. At higher temperatures, brook trout may have a competitive advantage over bull trout. Similarly, low temperatures may limit distributions of competitive species and result in only bull trout being present. Ziller (1992) studied creeks of the Sprague River subbasin, Oregon and reported that stream sections with August and September temperatures less than 5°C contained only bull trout, whereas brown trout and rainbow trout were found in sections with warmer temperatures. Brown trout and brook trout have similar temperature preferences, and similar upper lethal limits (MacCrimmon and Marshall 1968; MacCrimmon and Campbell 1969; Coutant 1977) and habitat use (Nyman 1970; Fausch and White 1981). Interspecific competition, mediated by temperature, may thus play an important role in bull trout distribution and abundance. A more detailed combination of field and laboratory studies is needed to test this hypothesis.

Other factors may influence the number of juvenile bull trout in streams. Low productivity, which was characteristic of all streams included in this study, may act to limit juvenile densities by regulating the amount of food available. In addition, canopy cover may limit the amount of solar input, thus reducing aquatic production and food for fish. Low numbers of aquatic insects and little algal growth was observed in North Gold Creek indicating low productivity, probably because of the almost complete canopy cover. Subsequently, low productivity, resulting in little food, may reduce the number of juvenile bull trout which can survive in North Gold Creek. Conversely, Gold

Creek is largely spring fed with low temperatures and little canopy cover. Gold Creek had abundant potential food and the highest density of juvenile bull trout.

A shortage of spawning habitat is another factor that can limit abundance of juvenile fish. In this study, only Grouse Creek appeared to be limited in spawning habitat (Figure 6). Grouse Creek,

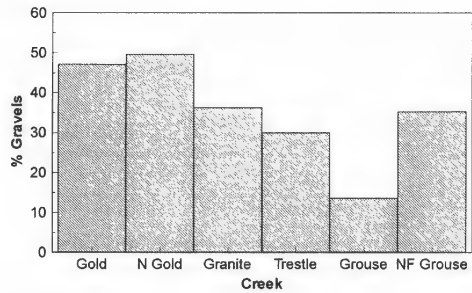


Figure 6. Percent of stream bed dominated by pea gravel and gravel in six streams of the Lake Pend Oreille drainage.

however, also had high maximum summer temperatures and very low conductivities, both of which might also result in lower densities of bull trout.

Results of this study indicate that juvenile bull trout 1) use habitat differently depending on their age (size), 2) increased in density with increasing number of pocket pools in a stream reach, and 3) were associated with stream reaches that had cool temperatures. Age 0 bull trout did not select for a particular habitat type and were mostly found in the channel margins. Age ≥ 1 bull trout selected pools, avoided riffles, and were mostly found in the main channel. Pocket pools were important because they may have provided additional feeding and resting areas. The highest densities of juvenile bull trout were in reaches within Trestle and Gold Creeks which had maximum summer temperatures ranging from 10 to 13.9°C. Although the relationship between temperature and density of juvenile bull trout was inconclusive in this study, other investigators have had similar results with bull trout and closely related species. Further investigation is needed to determine the influence of temperature on the density of bull trout (and other salmonids) during summer.

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Literature Cited

- Allan, J. H., 1980. Life history notes on the Dolly Varden charr (*Salvelinus malma*) in the upper Clearwater River, Alberta. Alberta Energy and Natural Resources, Fish and Wildlife Division, Red Deer, Alberta, Canada.
- Bisson, P. A., J. L. Nielsen, R. A. Palmason and L. E. Grove. 1981. A system of naming habitat in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62 - 73 in N. B. Armantrout, editor, Acquisition and Utilization of Aquatic Habitat Inventory Information. Proceedings of a Symposium, October 28-30, 1981, Portland Oregon. Hagen Publishing Company, Billings, Montana. Pages 62-73.
- Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423-438.
- Bonneau, J. L. 1994. Seasonal habitat use and changes in distribution of juvenile bull trout and cutthroat trout in small, high gradient streams. M. S. Thesis. University of Idaho, Moscow.
- Cardinal, P. J. 1980. Habitat and juvenile salmonid populations in streams in logged and unlogged areas of southeastern Alaska. M. S. Thesis, Montana State University, Bozeman.
- Carl, L. 1985. Management plan for bull trout in Alberta. Pages 71-80 in D. D. MacDonald, editor, Proceedings of the Flathead River Basin bull trout biology and dynamics modeling information exchange. Fisheries Branch, British Columbia Ministry of Environment, Cranbrook, British Columbia.
- Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American Northwest. California Fish and Game 64(3):139-174.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmon and trout in streams, with special reference to food and feeding. Pages 153-176 in T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan lecture series in fisheries, University of British Columbia, Vancouver.
- Coutant, C. C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34:739-745.
- Dambacher, J. M., M. W. Buktenica, and G. L. Larson. 1992. Distribution, abundance, and habitat utilization of bull trout and brook trout in Sun Creek, Crater Lake National Park, Oregon. Pages 30-36 in Howell, P. J. and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis.
- Enk, M. 1985. Modelling the effects of forest sediment on bull trout. Page 5 in D. D. MacDonald, editor. Proceedings of the Flathead River basin bull trout biology and population dynamics modelling exchange. British Columbia Ministry of the Environment, Fisheries Branch, Cranbrook, British Columbia.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.
- Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.
- Fraley, J. J., and B. B. Shepard. 1989. Life history, ecology and population status of migratory bull trout, (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Science 63:133-143.
- Goetz, F. 1989. Biology of the bull trout *Salvelinus confluentus*; a literature review. Willamette National Forest, Eugene, Oregon.
- Hahn, P. K. J. 1977. Effects of fluctuating and constant temperatures on behavior of steelhead trout (*Salmo gairdneri*). Ph. D. dissertation. University of Idaho, Moscow.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequence. Ecology 54:427-432.
- Hoelscher, B., and T. C. Bjornn. 1989. Habitat, densities, and potential production of trout and char in Lake Pend Oreille tributaries. Idaho Department of Fish and Game, Job Completion Report Project F-71-R-10.
- Horner, N. J. 1978. Survival, densities, and behavior of salmonid fry in streams in relation to fish predation. M. S. thesis. University of Idaho, Moscow.
- Jensen, J. W. 1981. Anadromous arctic char *Salvelinus alpinus*, penetrating southward on the Norwegian coast. Canadian Journal of Fisheries and Aquatic Sciences 38:247-249.
- MacCrimmon, H. R., and T. L. Marshall. 1968. World distribution of brown trout (*Salmo trutta*). Journal of the Fisheries Research Board of Canada 25:2527-2548.
- MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout (*Salvelinus fontinalis*). Journal of the Fisheries Research Board of Canada 26:1699-1725.
- Markle, D. F. 1992. Evidence of bull trout x brook trout hybrids in Oregon. Pages 58-67 in Howell, P. J. and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis.

- McPhail, J. D., and C. B. Murray. 1979. The early life-history and ecology of Dolly Varden (*Salvelinus malma*) in the upper Arrow Lakes. Department of Zoology and Institute of Animal Resources, University of British Columbia, Vancouver, British Columbia.
- Meisner, J. D. 1990. Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. *Transactions of the American Fisheries Society* 119:282-291.
- Moore, K. M. S., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1921-1930.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541-545.
- Nyman, O. L. 1970. Ecological interaction of brown trout (*Salmo trutta*) L., and brook trout (*Salvelinus fontinalis*) (Mitchill), in a stream. *Canadian Field Naturalist* 84:343-350.
- Overton, K. in review. R1/R4 standardized stream habitat inventory guide. United States Department of Agriculture, Forest Service, Intermountain Research Station, Boise, Idaho.
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream riparian and biotic conditions, U.S. Forest Service, Forestry and Range Experimental Station, General Technical Report INT-138, Ogden Utah.
- Pratt, K. L. 1984. Habitat use and species interactions of juvenile cutthroat (*Salmo clarki lewisi*) and bull trout (*Salvelinus confluentus*) in the Upper Flathead River basin. M. S. Thesis, University of Idaho, Moscow.
- Pratt, K. L. 1985. Pend Oreille trout and char life history study. Idaho Department of Fish and Game, Boise.
- Redmond, M. A. 1975. Natural production. International Atlantic Salmon Foundation Special Publications Series 6:134-135.
- Ricker, W. 1934. An ecological classification of certain Ontario streams. University of Toronto Studies, Biological Series 37. Publication of Ontario Fisheries Research Laboratory 49:7-14.
- Rode, M. 1988. Bull trout, *Salvelinus confluentus* (Suckley), in the McCloud River, status and recovery recommendations (draft). Inland Fishing Administration Report, California Department of Fish and Game, Sacramento.
- Saffel, P. D. 1994. Habitat Use by Juvenile Bull Trout in Belt-Series Geology Watersheds of Northern Idaho. M. S. Thesis. University of Idaho, Moscow.
- Scott W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. *Journal of the Fisheries Research Board of Canada*, Bulletin 184.
- Shepard, B., K. Pratt, and J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River Basin, Montana. Montana Department of Fish, Wildlife, and Parks, Kalispell.
- Sullivan, D. 1986. Hydraulics and fish habitat in relation to channel morphology. Ph. D. dissertation. Johns Hopkins University, Baltimore, Maryland.
- Wallis, O. L. 1948. Trout studies and a stream survey of Crater Lake National Park. M.S. Thesis. Oregon State University, Corvallis.
- Zar, J. H. 1984. Biostatistical analysis. Prentice Hall Incorporated, Englewood Cliffs, New Jersey.
- Ziller, J. S. 1992. Distribution and relative abundance of bull trout in the Sprague River Subbasin, Oregon. Pages 18-29 in Howell, P. J. and D. V. Buchanan, editors. *Proceedings of the Gearhart Mountain bull trout workshop*. Oregon Chapter of the American Fisheries Society, Corvallis.

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Jinfan Duan, Forest Engineering Department, Oregon State University, Corvallis, Oregon 97331

Alok K. Sikka, Forestry Sciences Laboratory, Oregon State University, Corvallis, Oregon 97331

and

Gordon E. Grant, Pacific Northwest Research Station, U.S. Forest Service, Corvallis, Oregon 97331.

A Comparison of Stochastic Models for Generating Daily Precipitation at the H. J. Andrews Experimental Forest

Abstract

Estimates of precipitation are often required to model hydrologic and ecologic processes. A variety of methods can be found in the literature for modeling the occurrence and distribution of daily precipitation amounts. Here we test their applicability against empirical data for the H. J. Andrews Experimental Forest in Oregon. A stochastic model for generating daily precipitation was developed using a two state Markov chain model for occurrence of precipitation. Five different theoretical distributions for the precipitation amount were compared, using data from the Andrews Experimental Forest in the Western Cascades of Oregon. Of the distributions examined (exponential, calibrated Weibull, calibrated beta-P, and two 2-parameter gamma distributions), the calibrated Weibull distribution and two parameter gamma distribution appear to be better for simulating daily precipitation amounts. Such models can be used to generate precipitation input to process-based deterministic hydrologic models useful for simulating hydrologic and ecologic responses to cumulative watershed effects.

Introduction

Stochastic models for generating daily precipitation are frequently used in a variety of hydrologic, ecologic, geomorphic, and water resources studies. These models rely on assumptions about the probability distribution of rainfall for a particular landscape. Such models are useful for extending meteorologic and hydrologic records beyond the timeframe of empirically measured values, filling in missing data at long-term measurement sites, and synthesizing records for unmeasured watersheds. The output from stochastic precipitation models can be used, in turn, as input to hydrologic and ecologic models that predict soil moisture, runoff, or the availability of water for plants.

Here we describe developing a model for generating precipitation data as input to process-based deterministic hydrologic models at the H. J. Andrews Experimental Forest (HJAEF). The Forest, which is located in the western Cascades of Oregon, and is a Long Term Ecological Research (LTER) site funded by the National Science Foundation (NSF). A major topic of research at the HJAEF is the relationship among hydrologic, ecologic, and geomorphic processes. While precipitation and other climate data has been recorded for more than 50 years at the Andrews, models to simulate precipitation are needed to extend that

record over century or longer timescales associated with forest succession, disturbance, and other ecological processes.

A variety of models can be found in the literature for simulating daily precipitation (Todorovic and Woolhiser, 1974; Smith and Schreiber, 1974; Chin, 1977; Buishand, 1978; Roldan and Woolhiser, 1982; Richardson and Wright, 1984). Due to the complex nature of rainfall processes, any rainfall model involves simplified assumptions of the process. For most practical problems, the model that best describes the precipitation distribution and amounts is preferred (Richardson, 1982). Our purpose here is to test a variety of models with different underlying assumptions against the actual data in order to select the best model or models to use for the HJAEF. We expect that the models that work best for the HJAEF will also be most appropriate for other watersheds in the western Cascades with similar precipitation regimes.

Models for generating daily rainfall sequences typically use a separate process for the rainfall occurrence (wet-dry event) and another process for the rainfall amounts on wet days (Todorovic and Woolhiser, 1974; Buishand, 1978; Richardson, 1982). Several approaches have been used for describing the occurrence of rainfall and the

distribution of rainfall amounts given the occurrence of rain (Buishand, 1978; Roldan and Woolhiser, 1982; Woolhiser and Roldan, 1982; Richardson, 1982). For the rainfall occurrence, the Markov chain and the alternating renewal process (ARP) have been generally used for modeling wet- dry day sequences. In particular, the Markov chain model is used extensively for daily precipitation (Gabriel and Neuman, 1962; Haan et al., 1976; Smith and Schreiber, 1974; Roldan and Woolhiser, 1982; Richardson and Wright, 1984). Buishand (1978), and Roldan and Woolhiser (1982) reported advantages of using the Markov chain model over the ARP model. They reported that the generation of synthetic sequences is simpler for a Markov chain and its parameters can be obtained more easily than for the ARP model.

The most common approach for describing the distribution of rainfall amounts on days with rain is to ignore the serial autocorrelation and consider that rainfall amounts are serially independent and to fit some theoretical distribution to the precipitation amounts (Todorovic and Woolhiser, 1974, 1975; Woolhiser et al., 1973; Smith and Schreiber, 1974; Richardson, 1982). Various probability density functions ranging from single parameter to multiple parameters have been proposed to describe the distribution of rainfall amounts (Todorovic and Woolhiser, 1974, 1975; Smith and Schreiber, 1974; Richardson, 1982; Woolhiser and Roldan, 1982; Pickering et al., 1988). Woolhiser and Roldan (1982) compared the chain-dependent (i.e. precipitation amounts are independent but the distribution depends on the state of the previous day) and independent exponential, gamma, and three parameters mixed exponential distributions and showed that the independent mixed exponential was the best for five U.S. stations. It should be noted that the single parameter models are more appealing for their simplicity and ease of parameterization. However, there is no general consensus on the performance or applicability of a specific model; choice of an appropriate model depends on the underlying distribution for the observed data. This suggests a need of examining different distributions and building a precipitation model for a site.

In this study, a first-order Markov chain with two states, wet or dry, was used for simulating the occurrence of precipitation. A continuous distribution function was used to model the amount of precipitation given that a day is wet. To ac-

complish this, five probability distributions for the precipitation amount (the exponential, calibrated Weibull, calibrated beta-P, and 2-parameter gamma distribution with two different estimators) were compared, using data from the HJ Andrews Experimental Forest in the Western Cascades of Oregon. The performance of these models in simulating daily and monthly precipitation at the Andrews Forest is presented.

The Models

Occurrence Process

Occurrence of precipitation is described by a two state Markov chain (day is wet or dry) of first order; that is, the probability of precipitation on a given day depends solely on whether or not precipitation occurred on the previous day. This approach has been used successfully and studied extensively to generate rainfall (Bailey, 1964; Haan, 1977; Richardson, 1981; Roldan and Woolhiser, 1982). The transition matrix is defined by:

$$P = \begin{bmatrix} p_{dd} & p_{dw} \\ p_{wd} & p_{ww} \end{bmatrix} \quad (1)$$

where p_{dd} , p_{dw} , p_{wd} , p_{ww} , are the conditional probabilities of a dry day following a dry day, a wet day following a dry day, a dry day following a wet day and a wet day following a wet day, respectively. A day with total rainfall of 0.0254 centimeters (0.01 inch) or more was considered a wet day. Since $p_{dd} + p_{dw} = 1$ and $p_{wd} + p_{ww} = 1$, P is fully defined given p_{dw} and p_{ww} . The occurrence is determined by comparing a generated random number with the elements of the probability transition matrix. If the previous day is dry, then a generated random number less than p_{dw} represents rain on the current day; and if the previous day is wet, a generated random number less than p_{ww} means the current day is also wet. Otherwise, the current day is a dry day.

Precipitation Amounts

Rainfall amounts are considered serially independent. Five different models of the distribution of daily rainfall amounts are used and compared. Seasonal variations of precipitation are determined by assuming that the model parameters are constant within a month and different between months.

Single parameter models

The exponential distribution is probably the most widely used single parameter model of daily precipitation amounts for its simplicity, invertibility and relatively good fit (Todorovic and Woolhiser, 1974; Richardson, 1981; Pickering et al., 1988). The cumulative distribution function of the exponential is given by

$$F(x) = 1 - e^{-\frac{x}{\lambda}} \quad (2)$$

Where x is the daily precipitation, $F(x)$ is the probability of events less than x , and $\lambda = E(X)$ is expectation of daily precipitation.

Single parameter probability distributions have also been derived by calibrating multi-parameter distributions (Pickering et al., 1988; Selker and Haith, 1990). Pickering et al. (1988) derived a single parameter model by calibrating a special case of the beta-P distribution model. In its most general form, beta-P is a three parameter model. The cumulative distribution function of the calibrated beta-P model of Pickering et al. (1988) is given by:

$$F(x) = 1 - \left(1 + \frac{x}{9\lambda}\right)^{-10} \quad (3)$$

A member of the Weibull family of distributions was given by Rodriguez (1977) as:

$$F(x) = 1 - e^{-\left[\frac{\Gamma(1+\frac{1}{c})x}{\lambda}\right]^c} \quad (4)$$

where c is a constant and $\Gamma(\cdot)$ denotes complete gamma function.

The calibrated Weibull distribution was presented by Selker and Haith (1990) based on the above equation. With $c=0.75$, as the optimized value for the data from Eastern USA, they derived the probability distribution for wet day given by:

$$F(x) = 1 - e^{-(1.191 \frac{x}{\lambda})^{0.75}} \quad (5)$$

In this study, we calibrated this model using Andrews Forest data to obtain optimized values of the parameters, which is discussed in the next section.

Multi-parameter models

Multi-parameter distributions such as the 2-parameter gamma, the 3-parameter gamma, the 3-

parameter mixed exponential, and others have been used (Mielke and Johnson, 1974). Multi-parameter models are generally considered to describe the distribution of precipitation amounts better than the one-parameter exponential distribution because of the greater flexibility obtained with the large number of parameters. The choice of model depends on the parsimony of parameters and ease of estimating parameters. Richardson (1982) suggested that unless the mixed exponential distribution has a clear advantage over the 2-parameter gamma distribution, the gamma distribution should be the appropriate choice of models for most applications.

The 2-parameter gamma distribution is used here with the general form of the probability density function given by:

$$f(x) = \frac{x^{\alpha-1} e^{-\frac{x}{\beta}}}{\beta^{\alpha} \Gamma(\alpha)} \quad (6)$$

where α and β are constants in gamma distribution. The gamma distribution is used with two different methods of parameter estimation. One method uses moment estimators (Devore, 1987), given by:

$$E(X) = \alpha\beta \quad (7a)$$

$$V(X) = \alpha\beta^2 \quad (7b)$$

where $E(\cdot)$ denotes the expectation and $V(\cdot)$ the variance of the data. The other method uses maximum likelihood estimators, with:

$$\alpha\beta = E(X) \quad (8a)$$

$$Y - \ln(E(X)) = E(\ln(X)) \quad (8b)$$

where Y is an intermediate value to be used in the following calculations.

There are a number of numerical schemes for determining the maximum likelihood estimators for the 2-parameter gamma (Thom, 1958; Greenwood and Durand, 1960; Mielke and Johnson, 1974; Choi and Wette, 1969). The numerical solution suggested by Choi and Wette (1969) was used in this study, which approximates the solution by Newton-Raphson iteration using the following equations:

$$\alpha_{i-1} = \alpha_{i-1} - \frac{\log(\alpha_{i-1}) - \Psi(\alpha_{i-1}) - Y}{\frac{1}{\alpha_{i-1}} - \Psi(\alpha_{i-1})} \quad (9a)$$

$$\Psi(\alpha) = \gamma - \frac{1}{\alpha} + \sum_{i=1}^{\infty} \frac{1}{(i+\alpha)} \quad (9b)$$

$$\Psi'(\alpha) = \sum_{i=0}^{\infty} \frac{1}{(i+\alpha)^2} \quad (9c)$$

where γ =Euler's Constant=0.57722157 and Ψ is Digamma function.

The above infinite summations are approximated using an arbitrary 10^{-7} criterion. If the difference between calculated value at time i and time $i-1$ is less than the criterion, then the value at time i is used. Since this numerical solution is always convergent with any initial value such that $0 < a_0 < \infty$ (Choi and Wette, 1969), an arbitrary number is given as a starting value in the computational estimation.

Experimental Design

The precipitation data of climatological station at Watershed #2 from H. J. Andrews Experimental Forest was used to calibrate and test the models since it has the longest observation history. The HJAEF is a mountain watershed of 6400 ha. Climate of the HJAEF is wet and fairly mild in the winter and warm and dry in summer, with

more than two-thirds of the precipitation falling between November through March (Bierlmaier and McKee, 1989). Climatological information has been collected at the HJAEF since 1951. Daily precipitation data from 1952 to 1992 was used in this analysis. Although precipitation can occur as rain or snow, this paper does not differentiate among these forms and only considers the liquid water equivalent.

For the calibrated Weibull distribution, a set of new parameter values for the HJAEF were obtained using a least Chi-square criteria. Simulations were made with a range of parameter (c) values between 0.5 and 1.5, with a step value of 0.01, and the Chi square values were computed. The parameter value which gave the least Chi square was selected as an optimized value (Figure 1). The following equation for the calibrated Weibull distribution was then used in this study:

$$F(x) = 1 - e^{-(1.052 \frac{x}{\lambda})^{0.9}} \quad (10)$$

In this study seasonal variations in the daily precipitation processes are assumed to be constant within a month and vary between months. Parameters are calculated based on monthly data; twelve sets of parameters for the five distribution

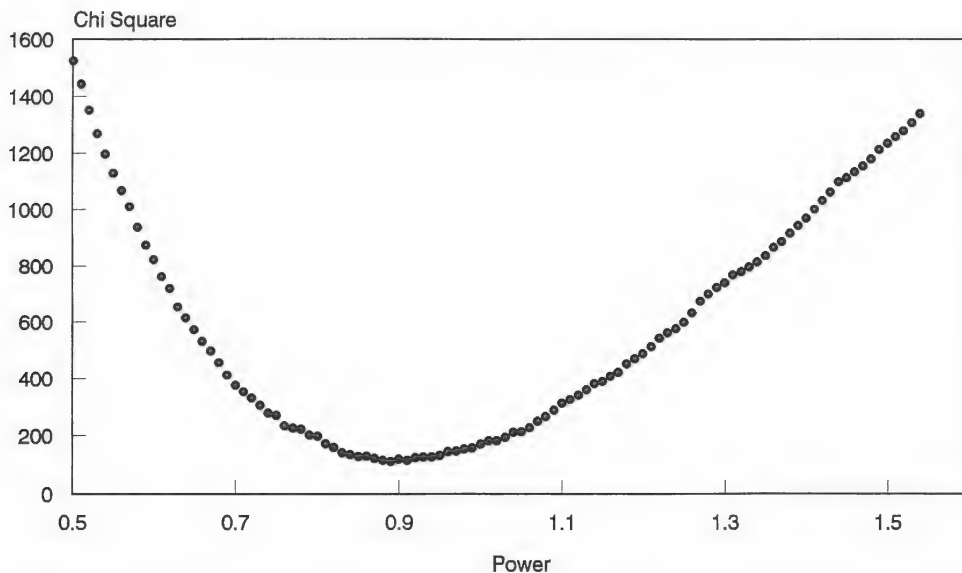


Figure 1. Calibration for constant c in general Weibull equation based on Chi square. Note minimum Chi square is at 0.90.

models were therefore obtained. Although there are complex techniques, such as finite Fourier series, to model seasonal variations (Roldan and Woolhiser, 1982), the simple technique used in this paper is reported to give fairly good results of distributions for wet days (Richardson, 1981). A summary of model parameters based on the 41 years of data is given in Table 1. The above precipitation models were then run for 41 years with five distributions of precipitation amounts. Daily amounts were summed to obtain monthly and annual precipitation amounts.

A Chi Square test was used to test and quantify the goodness-of-fit of the above models. For daily and monthly analyses, data were categorized into 51 bin cells. It was made sure that each bin cell possessed at least 5 occurrences. A Chi-square tested whether the two data sets came from the same population by:

$$\chi^2 = \sum_{i=1}^n \frac{(\text{OBSERVED}_i - \text{SIMULATED}_i)^2}{\text{OBSERVED}_i + \text{SIMULATED}_i} \quad (11)$$

where SIMULATED and OBSERVED are number of events in a combined bin i ; n is the total number of bins constructed.

Since each term in a Chi-square sum is supposed to approximate the square of a normally distributed quantity with unit variance, the variance of the difference of two normal quantities is

the sum of their individual variances, not the average. So the denominator of the above Chi-square was modified from the regular equation (Press et. al., 1992).

The probabilities of the observed data and the simulated data belonging to same distribution were calculated using the equation:

$$\text{Prob} = \frac{\Gamma\left(\frac{n}{2}, \frac{\chi^2}{2}\right)}{\Gamma\left(\frac{n}{2}\right)} \quad (12)$$

where $\Gamma(\dots)$ denotes incomplete gamma function. A better model should give lower Chi-square values and high probability values. Table 2 shows the results of the Chi-square test used for daily and monthly data.

Results and Discussion

The analysis of 41 years of observed precipitation data from the HJAEF shows that about 55% of days were dry days (precipitation less than 0.01 inch). The distribution of relative frequencies of daily rainfall amounts, as shown in Figure 2, has a reversed J-shaped exponential distribution with the smaller amounts occurring more frequently than the larger amounts. Percentage of days with precipitation was highest from October though March (about 60%), with the wet day average

TABLE 1. Parameters of H. J. Andrews Precipitation Model.

Month	Daily Mean (cm)	Variance (cm)	Prob. of Dry to Wet	Prob. of Wet to Wet	Prob. of Wet Day	α for Moment Estimator	β for Moment Estimator	α for Maximum Likelihood Estimator	β for Maximum Likelihood Estimator
1	1.791	1.514	0.327	0.816	0.64	0.833	0.846	0.914	0.771
2	1.575	1.171	0.345	0.785	0.616	0.835	0.743	0.901	0.688
3	1.339	0.683	0.336	0.793	0.619	1.032	0.511	1.027	0.513
4	0.937	0.465	0.319	0.741	0.552	0.744	0.496	0.959	0.385
5	0.838	0.282	0.223	0.680	0.410	0.982	0.336	1.069	0.308
6	0.709	0.279	0.168	0.599	0.295	0.709	0.394	0.988	0.283
7	0.488	0.137	0.064	0.466	0.107	0.684	0.281	1.034	0.186
8	0.729	0.208	0.074	0.584	0.150	1.002	0.286	1.109	0.259
9	1.046	0.505	0.125	0.607	0.241	0.854	0.483	0.946	0.436
10	1.420	0.973	0.199	0.682	0.385	0.814	0.686	0.874	0.639
11	1.892	1.580	0.367	0.781	0.626	0.892	0.835	0.954	0.781
12	1.918	1.715	0.368	0.788	0.634	0.844	0.894	0.900	0.839

TABLE 2. Chi-square Test Result.

Chi-Square value						Probability of belonging to same distribution					
Month	Degrees of Freedom	Exponential	Weibull	Beta-P	Gamma Moments Estimator	Gamma Maximum Likelihood	Exponential	Weibull	Beta-P	Gamma Moments Estimator	Gamma Maximum Likelihood
Daily Precipitation Amounts											
1	41	46	23.31	38.84	19.81	38.47	0.27	0.99	0.57	1	0.58
2	37	49.79	34.85	44.35	31.25	34.08	0.08	0.57	0.19	0.73	0.61
3	28	36.7	28.94	43	36.85	36.66	0.13	0.42	0.03	0.12	0.13
4	26	33.62	48.34	38.2	39.64	35.59	0.14	0	0.06	0.04	0.1
5	24	29	17.63	25.8	25.55	33.81	0.22	0.82	0.36	0.38	0.09
6	20	28.6	19.3	26.81	20.87	25.4	0.1	0.5	0.14	0.4	0.19
7	13	13.9	13.16	14.81	11.05	15.64	0.38	0.44	0.32	0.61	0.27
8	17	17.75	13.01	20.97	17.75	18.88	0.4	0.74	0.23	0.4	0.34
9	21	38.29	25.03	28.58	27.61	34.12	0.01	0.25	0.12	0.15	0.04
10	31	43.19	26.75	36.08	28.18	32.93	0.07	0.68	0.24	0.61	0.37
11	51	41.77	45.08	33.23	37.95	28.7	0.82	0.71	0.97	0.91	1
12	51	37.68	37.65	52.51	31.48	37.54	0.92	0.92	0.42	0.99	0.92
mean		34.69	27.76	33.6	27.33	30.99	0.3	0.59	0.3	0.53	0.38

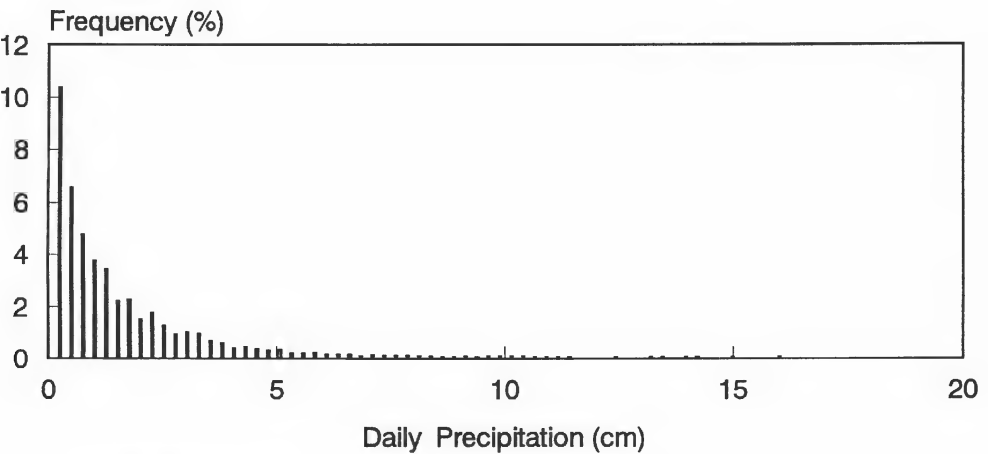


Figure 2. Observed daily precipitation distribution at HJA.

amount of precipitation being larger (about 0.8 inch) than that in the months from April to September (less than 0.5 inch), as shown in Figure 3a. The variance of daily precipitation was also higher in the wet season (October through March).

The conditional probabilities of wet day precipitation (Figure 3b) demonstrate the persistence of daily precipitation events. In the wet season, a wet day is more likely to be followed by a wet

day, while in the dry season (April through September), the probability of a dry day following a dry is much higher than a wet day following a dry day. The first-order Markov chain model simulated 8,231 dry days (about 55.0% of total days), which is very close to the actually observed 8,255 dry days (about 55.1% of total days). A comparison of the observed and simulated wet spell frequency distribution is shown in Figure 4. This

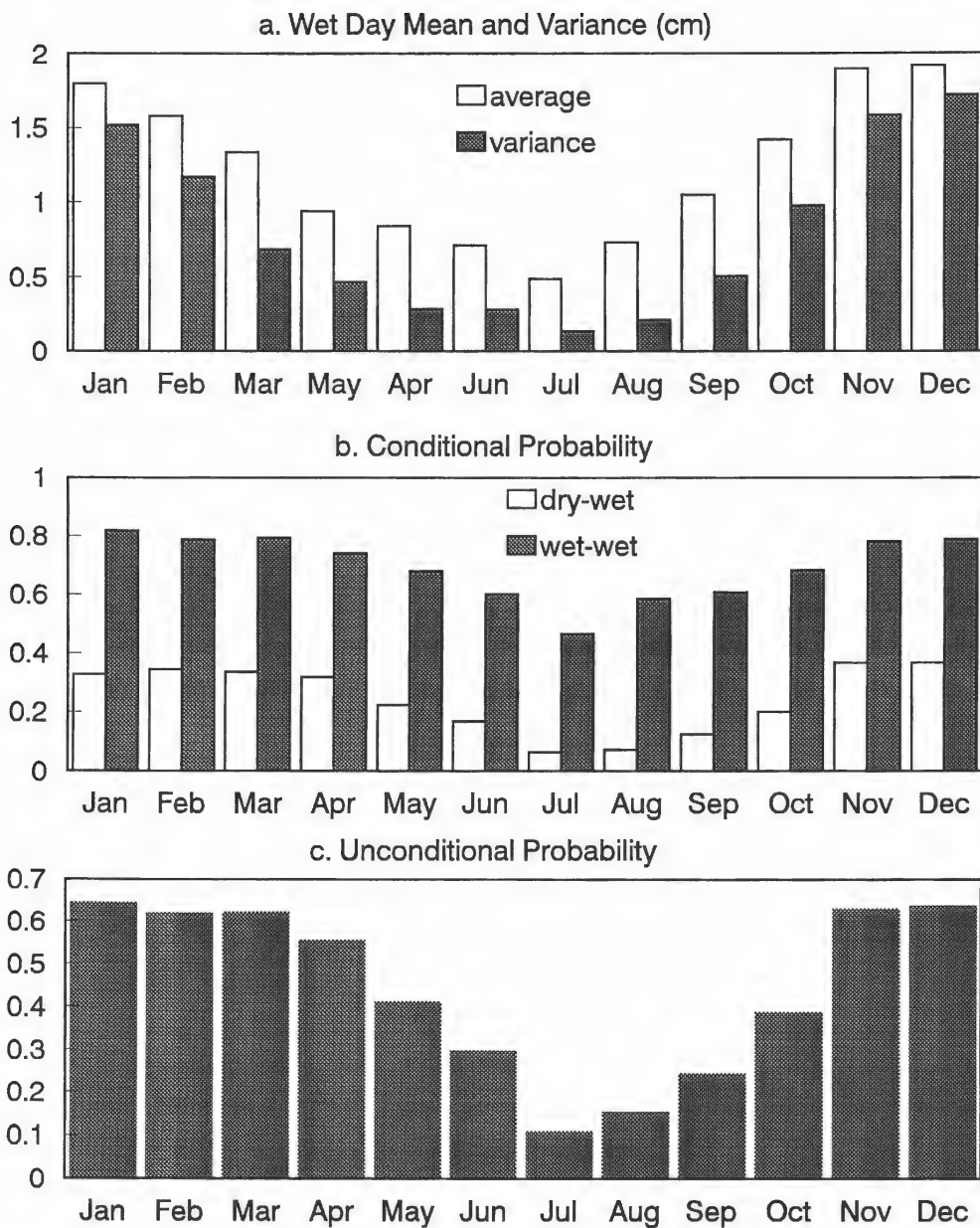


Figure 3. Model parameters for H. J. Andrews Experimental Forest.

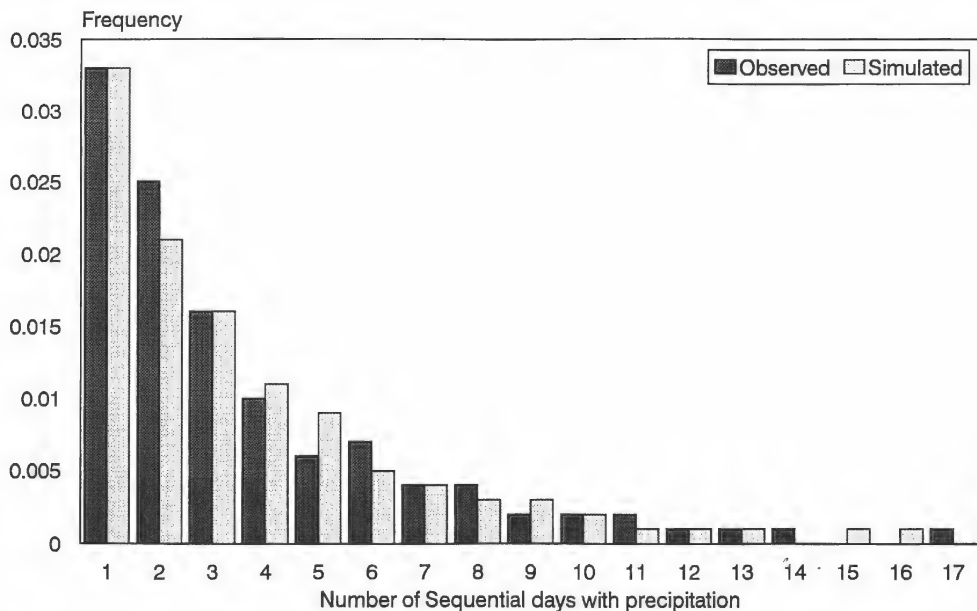


Figure 4. Markov chain performance. The true probability of a dry day observed is 55.1% and for simulated is 55.0%.

shows a close comparison of the occurrence of simulated wet days with the observed data.

Daily precipitation distributions of observed and model simulated data with different models are shown in Figure 5a. The results generated by all models closely approximate the observed data. The monthly distribution of precipitation amounts obtained by summing the daily precipitation amounts generated with each model is also shown (Figure 5b). Visually, for daily and monthly precipitation amounts, all the above models generally represent the observed data well.

To compare model performance, the summary of Chi-square test results is given in Table 2. Model performance in terms of Chi-square probabilities of different models for daily and monthly precipitation amounts is shown in Figure 6. For simulation of daily amounts, the two parameter gamma and calibrated Weibull (with higher mean probability of about 0.52 and lower Chi-square of about 29) appear better than exponential and Beta-P distributions. However, none of the above models was good at simulating daily amounts in March and April. It appears that the models tend to break down during the transition from a wet to a dry season. This may be due to the changes in

the underlying process of precipitation mechanism during the transition period. For simulating monthly amounts, all the above models in general appear to perform well. The 2-parameter gamma, with moments estimator showed better results than the maximum likelihood estimator.

The distribution of daily maximum precipitation obtained from each model are compared with the observed data in Figure 7. The gamma with maximum likelihood estimator and exponential appear closer to the observed data. These results suggest that the two parameter gamma with moment estimator and calibrated Weibull should be acceptable for generating daily rainfall data for general hydrologic, ecologic, and water yield studies at the HJAEF. However, the single parameter calibrated Weibull distribution is easy to apply and equally good. The gamma distribution with maximum likelihood estimator may be preferred for conducting hydrologic studies that are sensitive to daily extreme precipitation amounts.

Our results are based on the data from the HJAEF. These results may be applicable to other areas in the western Cascades of Oregon which have similar climate. A further study is in progress to conduct this analysis for a number of

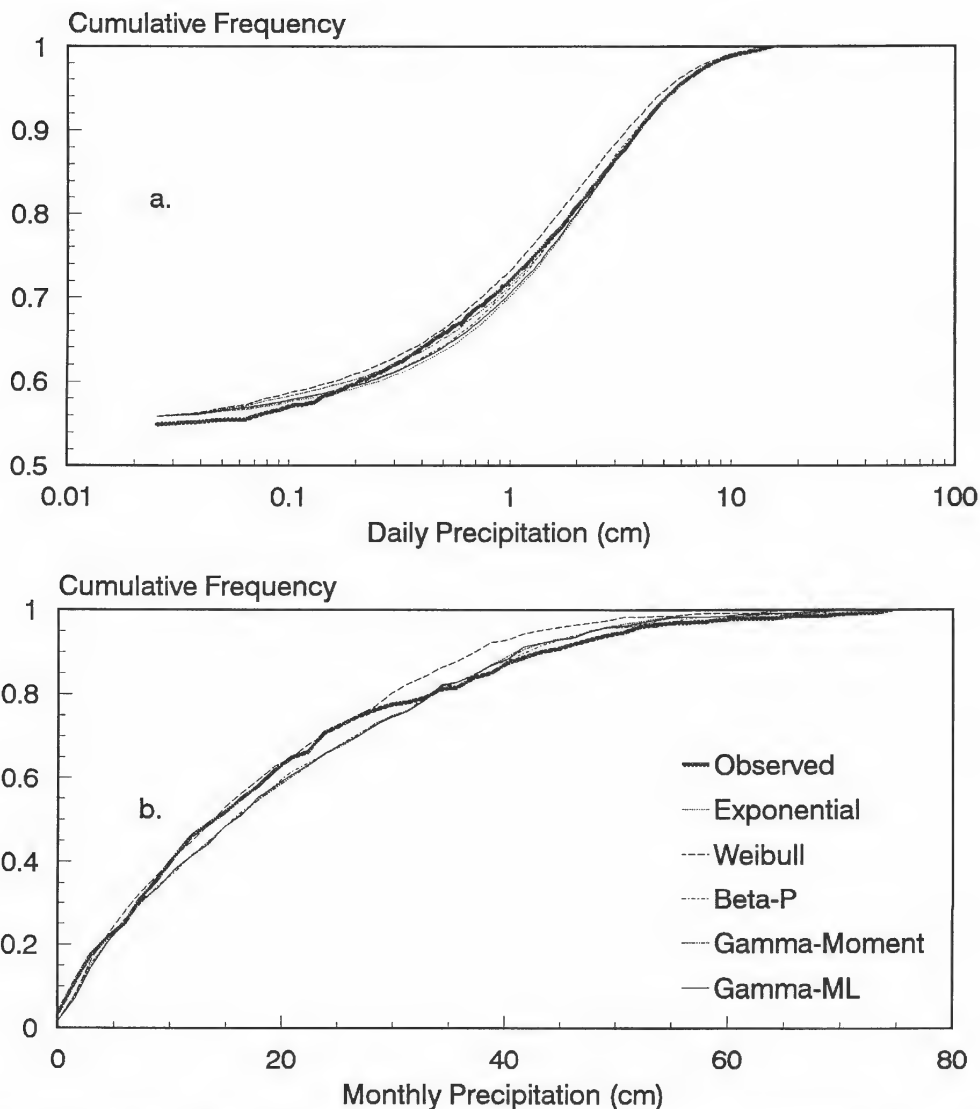


Figure 5. Comparison of observed daily and monthly amounts with models. a). Cumulative frequency for daily amount; b). cumulative frequency for monthly amount.

precipitation sites in the western Oregon, and examine the general applicability of these results to regional studies.

Conclusion

A daily precipitation model has been presented for generating daily precipitation for the H. J.

Andrews Experimental Forest, based on a two-state Markov chain governing the occurrence and a theoretical distribution governing the amounts of precipitation. The exponential, calibrated Weibull, calibrated Beta-P, and two 2-parameters gamma distributions are compared in generating precipitation amounts. The Markov chain model performed well at simulating daily precipitation

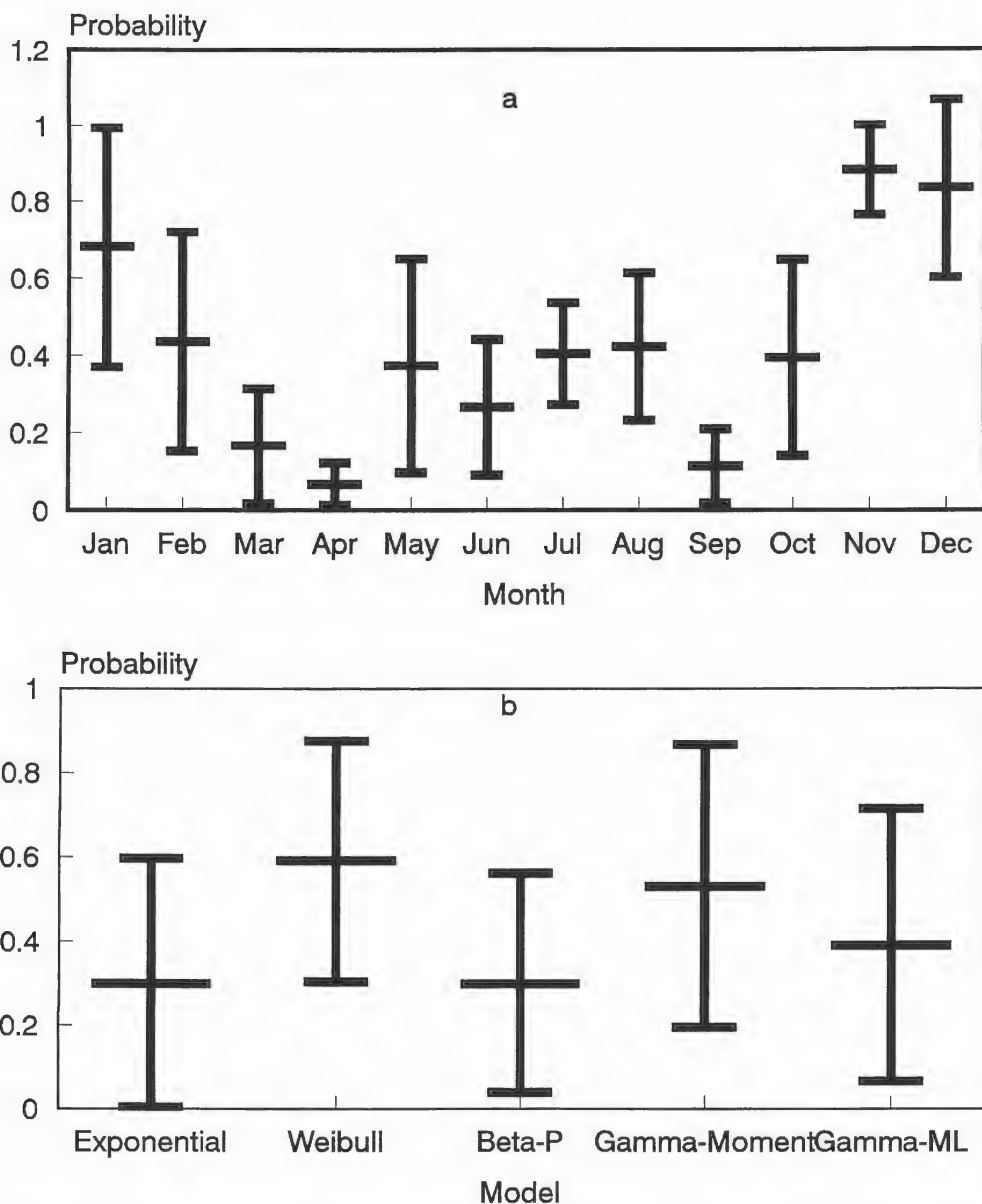


Figure 6. Model performance. a). Comparison of behavior of all 5 models combined by month; b). total probability by model for all months combined. Note mean and one standard deviation plotted.

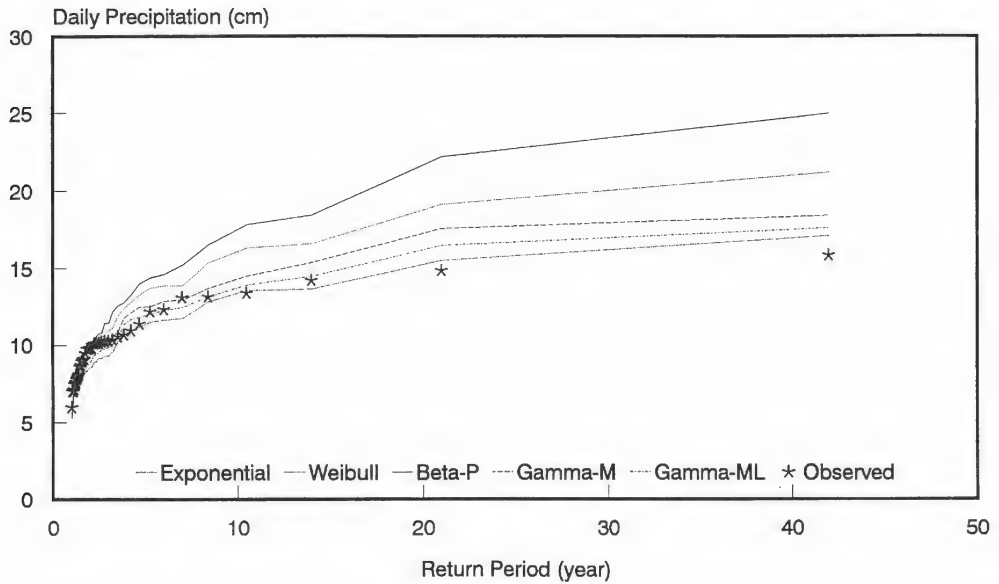


Figure 7. Comparison shows that gamma with maximum likelihood estimator and exponential appear better in generating daily extreme precipitation.

occurrences. The results also suggest that the calibrated Weibull is appropriate for generating daily precipitation amounts for its simplicity, goodness-of-fit and reversibility. The 2-parameters gamma may be preferred if the accuracy of daily amounts as well as daily extreme values are also important in a given study.

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Literature Cited

- Bailey, N. T. J., 1964. The elements of stochastic processes. John Wiley, New York, pp39.
- Bierlmaier, F. A. and Art McKee, 1989. Climatic summaries and documentation for the primary meteorological station, H. J. Andrews Experimental Forest, 1972-1984, USDA Forest service, Pacific Northwest Research Station, Portland, OR, General Technical Report. PNW-GTR-223, pp26.
- Buishand, T. A., 1978. Some remarks on the use of daily rainfall models. *Journal of Hydrology*, 36:295-308.
- Chin, E. H., 1977. Modeling daily precipitation occurrence process with Markov chain. *Water Resour. Res.* 13(6): 949-956.
- Choi, S. C. and R. Wette, 1969. Maximum likelihood estimation of the parameters of the Gamma distribution and their bias. *Technometrics*, 11(4):683-690.
- Devore, Jay. L., 1987. Probability and statistics for engineering and the sciences. Brooks/Cole Publishing company, Monterey, California, pp672.
- Gabriel, R. and J. Neuman, 1962. A Markov chain model for daily rainfall occurrence at Tel Aviv, Israel. *Q. J. R. Meteorol. Soc.* 88:90-95.
- Greenwood, Anther J. and David Durand, 1960. Aids for fitting the Gamma distribution by maximum likelihood. *Technometrics* 2:55
- Haan, C. T., 1977. Statistic methods in hydrology. The Iowa State University Press, Ames, Iowa. pp378.

- Haan, C. T., D. M. Allen and J. O. Street, 1977. A Markov chain model of daily rainfall. *Water Resour. Res.* 12(3):443-449.
- Mielke, Paul W. Jr. and Earl S. Johnson, 1974. Some generalized distributions of the second kind having desirable application features in hydrology and meteorology. *Water Resour. Res.* 10(2):223-226.
- Pickering, N.B., J.R. Stedinger and D. A. Haith, 1988. Weather input for nonpoint source pollution models. *J. Irrig. Drain. Eng.* 114(4):674-690.
- Press, William H., Saul A. Teukolsky, William T. Vetterling and Brian P. Flannery, 1992. *Numerical Recipe* in C. Cambridge University Press, NY 10011-4211, pp 994.
- Richardson, C. W., 1981. Stochastic generation of daily precipitation, temperature, and solar radiation. *Water Resour. Res.* 17(1):182-190.
- Richardson, C. W., 1982. A comparison of three distributions for the generation of daily rainfall amounts. In: *Statistical analysis of rainfall and runoff*, pp. 67-78, V. P. Singh (ed.). Water Resources Publications, 700 pp.
- Richardson, C. W., and D. A. Wright, 1984. *WGEN: a model for generating daily weather variables*, U.S. Dep. Agric., ARS-8, 83p.
- Rodriguez, R. N., 1977. A guide to the Burr type XII distributions, *Biometrika.* 64:129-134.
- Roldan, Jose and D. A. Woolhiser, 1982. Stochastic daily precipitation models: 1. A comparison of occurrence processes. *Water Resour. Res.* 18(5):1451-1459.
- Selker, J. S. and D. A. Haith, 1990. Development and testing of single-parameter precipitation distributions. *Water Resour. Res.* 26(11):2733-2740.
- Smith, R. E., and H. A. Schreiber, 1974. Point processes of seasonal thunderstorm rainfall, 2. Rainfall depth probabilities. *Water Resour. Res.* 10(3):418-423.
- Thom, H.C.S., 1958. A note on the Gamma distribution. *Monthly Weather Rev.* 86(4):117-122.
- Todorovic, P. and D. A. Woolhiser, 1974. Stochastic model of daily rainfall, *Proceedings of the Symposium on Statistical Hydrology*, U.S. Dep. Agric. Misc. Publ. 1275, 232- 246.
- Todorovic, P. and D. A. Woolhiser, 1975. A stochastic model of n-day precipitation. *J. Appl. Meteorol.* 14(1):17-24.
- Woolhiser, D. A., E. Rove and P. Todorovic, 1973. Temporal and spatial variation of parameters for the distribution of n-day precipitation. In: *Flood and Droughts: proceedings of the Second International Symposium on Hydrology*, pp. 605-614, Water Resources Publications, Ft. Collins, Colorado.
- Woolhiser, D. A. and Jose Roldan, 1982. Stochastic daily precipitation models: 2. A comparison of distribution amounts. *Water Resour. Res.* 18(5):1461-1468.

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Hugh DeForest Safford, Division of Environmental Studies, Wickson Hall, University of California, Davis, California 95616

The Recovery Planning Blues

The 1973 Endangered Species Act, soon to be reviewed by the U.S. Congress, mandates that "recovery plans" be developed for species listed as threatened or endangered by the Department of the Interior or the Department of Commerce. Recovery plans are the blueprints for species conservation, but although they are essential to the convalescence of threatened and endangered biota, recovery strategies have been formally drafted for only half of all listed species, and many completed plans are seriously deficient for a variety of reasons; both scientific and political support for recovery planning as presently formulated is on the wane. In this paper, I review scientific criticism of the procedure, offer a number of recommendations for a meaningful revision of the recovery planning process, and reveal my (guarded) pessimism regarding the future of this crucial component of the United States' most important conservation law.

*

The purpose of the 1973 Endangered Species Act (ESA) is

...to provide a means whereby the ecosystems upon which endangered and threatened species depend may be conserved (and) to provide a program for the conservation of such endangered ... and threatened species... (16 U.S.C. Section 2 [b])

As originally intended, the ESA established as a policy of Congress that *all federal departments shall seek to conserve endangered and threatened species and use their authorities in furtherance of the Act.*

Although it was the product of a Republican administration and originally enjoyed strong bipartisan support, the ESA is today the target of a growing wave of conservative-based public hostility, centering on its severe, supposedly inflexible nature, and its putatively harmful effects on both economy and society. Whilst these "threats to economy and society" have been shown to be largely imaginary—if not downright fallacious (see Chadwick 1995, Meyer 1994, Barker 1993)—the fact remains that popular mistrust of the ESA and its apparent conflicts with Fifth Amendment property guarantees is at an all-time high. Paradoxically—and at a supremely inopportune time—the Act has recently come under great criticism from the scientific community as well, for precisely the opposite reasons that conservatives oppose it: many scientists and environmentalists believe that the ESA as presently formulated and/or implemented is simply too weak to combat the growing specter of species extinctions.

Most scientific criticism of the Endangered Species Act centers on the failings of the "recovery

process" as mandated in Section 7 (f). S. Winckler (1993) writes:

That it saves organisms from extinction is faint praise for a law with the far loftier aspiration of "better safe-guarding, for the benefit of all citizens, the Nation's heritage in fish, wildlife and plants." It is the stated purpose of the law not to just keep species from going extinct but to return them to viability. In this regard it is failing.

As Winckler observes, in practice the recovery planning process has been grossly ineffective: of 1354 species listed as threatened or endangered between the 1966 passage of ESA's forerunner, the Endangered Species Preservation Act, and 1992, only 19 species had been removed, *including eight listed in error and seven that became extinct* (GAO 1992). The situation is so discouraging, in fact, that a recent paper went so far as to state that "recovery plans ... (more) often manage for extinction ... than for survival" (Tear et al. 1993).

Biological criticism of the recovery planning process has taken two tacks. Some authors argue that the ESA itself is fundamentally flawed and needs major revision (see Rohlf 1991), while others contend that the ESA remains a strong legal tool, and that the recovery planning process (and the ESA in general) has failed more to lack of political will than to technical deficiencies (see O'Connell 1992). I take the heretical position that both sides are partly right, i.e. that the ESA could bear some fine-tuning and that some basic changes are necessary in the way the Act is applied, but I also believe that long-term species conservation in the United States is unlikely to be effective unless we can fundamentally alter the manner in which the American polity and economic system work. Sound like a tall order? It is, and one which I don't think Americans will easily make.

*

Although scientists may disagree as to what exactly should be done to remedy the ailing recovery planning process, there is surprisingly little discord regarding what is actually wrong. It is instructive that these seemingly antagonistic camps almost universally agree as to the major problems facing the recovery of threatened and endangered species in the United States today.

Although the stated purpose of the ESA is the conservation of the ecosystems upon which threatened and endangered species depend, species recovery priorities show little regard for conserv-

ing biodiversity as a whole. The U.S. Fish and Wildlife Service (USFWS) has shown an historical propensity to lavish an inordinate amount of resources "on either high-profile, low priority species, or on low priority tasks for high-priority species" (GAO 1988). This tendency continued even after GAO and Congressional criticism: in 1990, of \$102 million appropriated for 591 taxa, \$55 million went to only twelve species, while a total of \$28 million was shared among the 570 organisms lowest on the "charisma" totem pole (Winckler 1993); even with the recognition that many species truly *are* less expensive to protect, manage, and/or study, this fiscal discrepancy is appalling. As S.M. Meyer (1994) notes:

Focusing so much attention on the plight of a single "endangered species" ... trivializes the importance of preserving the remnants of America's natural heritage and encourages ridiculous metaphysical calculations: owls versus loggers, moss versus highways.

Many critics argue that the preservation of areas rather than species (and subspecies, distinct populations etc.) would not only simplify the task of protecting and recovering listed organisms, but would save American taxpayers millions of dollars as well (Tear et al. 1993, Craighead 1994, Meyer 1994, etc.). A case in point is the more than \$1 billion spent by tax-supported agencies in the (thus far) futile attempt to stem the decline of Pacific-run salmon species in the Northwest. Many experts agree that much of this money might have been saved if recovery efforts had focused more on mitigation of habitat and ecosystem degradation than on more localized, stop-gap measures like fish-ladder construction and hatchery-based restocking (see Maxwell 1992).

The protection of certain species, such as large predators (grizzly bear, gray wolf) that are extremely vagile and cover large territories, is often cited as an example of how single species listings could indirectly benefit other endangered and threatened species through an ecosystem-wide "umbrella" effect, but the protection of (entire) ecosystems as critical habitat upon which threatened or endangered species depend—apparently the specific intent of Congress in passing the ESA (see Section 2, e.g.)—has, thus far, foundered on political and economic opposition (Keiter 1989). I should note that, even in the face of such antagonism, some recent recovery plans have—laudably—begun to treat species with similar habitat requirements jointly, so as to focus recovery efforts

on ecosystem conservation rather than on "narrowly-focused species-by-species measures" (USFWS 1994a). One recovery plan from northern Florida colists 4 herbaceous plants based on "conservative assessments of threats to the ...area ecosystems;" the plan goes on to warn that "...unless conservation measures for these four are successful, further listing proposals will be necessary" (op. cit.). *Bravo*.

Although the designation and protection of critical habitat (required under Section 4) is technically part of the "listing" process, it has become, nonetheless, another point of great contention in the debate over ESA mandated recovery planning. It is generally recognized that habitat protection is the key to species preservation and that viable conservation schemes simply must seek to maintain natural habitat; recovery efforts centered on "habitat-less" species—particularly vertebrates—are very long shots indeed (Murphy et al. 1994). Nonetheless, the original concept of critical habitat probably would not have been defined if it had not been for judicial pressure exerted on the USFWS in cases such as the Mississippi sandhill crane listing in 1975 (see Yaffee 1982). Twenty years later, a random review by this author of twenty recovery plans released during 1994 and 1995 showed that 90% (18) considered habitat destruction, degradation, or modification the primary threat facing the species in question (in the other two cases, anthropically introduced animals were believed to represent the greatest threat [USFWS 1993a, USFWS 1993b]); even so, litigation remains disturbingly necessary to compel critical habitat designations (see, for example, the case of the desert tortoise [USFWS 1994b]).

Even though human activities are by far the primary cause of species endangerment (Schemske et al. 1994), ESA amendments and USFWS decisions have made it progressively easier for agencies and private concerns to bypass or challenge the otherwise stringent requirements of the Act. These loopholes include a 1978 amendment permitting agencies to exclude areas from critical habitat on economic or other grounds, and granting that the Secretary of the Interior need only define critical habitat if "prudent or determinable"; a 1982 amendment sanctioning the power of federal agencies (with concurrence of the USFWS) to make findings of "no adverse effect" vis-a-vis public works, *without formal interagency consultation or supporting biological rationale*; and the

present USFWS interpretation of the Section 7 (a) (2) prohibition of federal destruction or modification of designated critical habitat, which allows such action unless it threatens *both* the survival *and* the recovery of endangered and threatened species, rather than *either* of the two (!). Combined with substantial political pressure, these chasms in the law have led the USFWS to avoid critical habitat designation whenever possible (Rohlf 1991), making the attainment of recovery objectives all but impossible. In addition, although delays in the denomination of critical habitat cannot be directly blamed for the accompanying lethargy in recovery plan output, the disease may be contagious: by 1992, recovery plans themselves had been completed for just over half of all listed species, and most of these were prepared long after listing, an apparently direct violation of the intent of Section 4 (c) of the ESA as interpreted in various court cases (see especially, Northern Spotted Owl v. Lujan 1991). Many authors argue that recovery efforts, if they are implemented at all, are generally implemented too late to offer any reasonable hope of achieving long-term success (see Murphy et al. 1994); Tear et al. (1995), in a comprehensive review of all 314 recovery plans written by the USFWS and NMFS as of August 1991, found that an average of five years elapsed between completion of each step of the recovery plan process (listing to plan approval to final revision).

Recovery plans are also plagued with serious shortcomings in their conclusions as to what biological data are actually necessary for conserving threatened and endangered species. Schemske et al. (1994) reviewed 98 recovery plans for plant species produced between 1980 and 1992 and found that *not one* of them included "sufficient biological information to assess the dynamics of populations...of the species considered." Schemske et al. suggested a 3 step course of action for endangered plant recovery—their survey showed that only 1/3 of the plans met their first criterion (publication of demographic data), and none had addressed the remaining two steps (identification of life history stages with the greatest impact on population growth, and the elucidation of biological processes affecting these stages). My cursory review of recovery plans released since 1994 (see above) showed that this trend continues: rather than providing actual data for policy makers and plan managers, most plans merely *call* for the

publication of such data. Schemske et al. concluded that most listed species receive less protection under ESA than is necessary to ensure their long-term survival; see Tear et al. (1995) for an excellent treatment of this critical problem in existing recovery plans.

Metapopulations have been shortchanged in the preparation of most recovery plans (Rohlf 1991). Metapopulation dynamics are important not only for the survival of local populations but for long-term survival of many species as well, especially where regional rates of patch extinction and colonization are not in proper balance. This is especially true for species where both occupiable habitats and extant populations are few. Under present USFWS policy, distinct populations of listed species are not separately protected unless they have been listed separately (Rohlf 1991), and even then, only vertebrate populations are allowed this "luxury" (Section 9 also protects animal *individuals* [but not plant individuals], yet how this protection applies to metapopulations is unclear). This is a distinctly unsettling situation for most "nonequilibrium", r-selected species that may find themselves in trouble...

Finally, recovery plans are often begun so long after listing and after prolonged habitat destruction so severe that recovery goals are set below minimum viability (Tear et al. 1993); in fact, official population goals for some species have actually been set lower than the population size at the time of listing (Murphy et al. 1994)! In general, Schemske et al. (1994) found that recovery criteria are often based on contemporary population numbers and not on the actual "biological status" of the species. In addition, recovery plans have historically tended to discount low probability stochastic factors in their appraisal of long-term viability and requisite population sizes, even though "future, uncertain risks loom as significant threats to species persistence" (Rohlf 1991); word has it that this tendency is no longer as common as it was, but my review of recent recovery plans turned up only lip-service to the importance of random, uncontrollable events.

*

Although the recovery planning process is fraught with iniquity as far as many biologists are concerned, the fact remains that the greatest hurdle to species recovery is not the ESA itself, but rather the maelstrom of political and economic inter-

ests that compete to derail it at every opportunity. Funding for the ESA is clearly inadequate to even begin to list and plan recovery for the estimated 3800 species that require such action (O'Connell 1992), much less to implement those plans already in effect, or to inform and educate the public about the importance of species and ecosystem preservation; a recent study noted that the total amount of money needed to recover all listed species and to list and recover all current candidate species is approximately 50 times the present annual budget for ESA effectuation (Dwyer et al. 1995). Furthermore, although recovery plans are used in setting regional and national funding priorities and in justifying USFWS (as well as other agencies') appropriations in Congress, they cannot themselves commit resources to any part of plan implementation (USFWS 1990a). Recovery plans are best considered "broad-based planning documents", that exist to direct agency efforts "to develop specific actions from the broad concepts presented" (USFWS 1993c). Specific studies, programs and management actions are not developed until the implementation phase, and thus are subject to federal budgetary approval and appropriation, as well as to the discretion of whatever agency or regional office is finally charged with execution of the plan. Neither the recovery team, nor the USFWS have *any* enforcement authority in the final decision as to whether various parts of the plan's recommendations are implemented or not. As one recovery team put it: "Interagency cooperation is the key to successful implementation. ... *Implementation of recovery plans is always a good faith effort of all parties involved*" (USFWS 1993c) (*italics mine*).

This "good faith" stuff is what worries me. As long as our economic system continues to reward short-term exploitation while amercing longer-term, more restorative practices, and as long as government-funded disincentives to conservation continue to benefit small (yet politically powerful) sectors of the population (e.g. subsidized timber sales and below-cost grazing fees), "good-faith efforts" will necessarily fall short of sufficiently protecting our nation's biological legacy; as Paul Hawken eloquently demonstrates in *The Ecology of Commerce* (1993), the present ability of American business to externalize its costs onto society may maximize short-term return on capital, but—as a perverse result—the growth of corporate profits and the real enhancement of human and natural

welfare are ships bearing different courses. Distressingly, economically-motivated political manipulation of what is intended to be a biologically-driven process is so rampant that S.L. Yaffee, after closely studying the early history of the ESA and its implementation, could write:

The administration of (ESA and the recovery planning process) is laced with discretion and heavily influenced by the political context in which implementation takes place ... Whether an agency (decides) to incorporate endangered species objectives in planning, whether USFWS chooses to delay or modify rule-making, or whether a species receives protection depends (ultimately) on who is involved and what they have at stake (Yaffee 1982).

*

To say that the recovery process is flawed is not to say that the Endangered Species Act should be scrapped; quite the contrary. In this author's opinion, the prohibitory nature of the ESA is a necessary evil, for the fact remains "that we will always be plagued by ... self-indulgent individuals, groups and businesses that lack any sense of social responsibility" (Meyer 1994). Without the legislative compulsion of the ESA, rival interests would have no reason to solve what is—like it or not—a widespread and ever-worsening dilemma

of great biological and socioeconomic significance. I submit that most of the deficiencies outlined above could be remedied through a general policy of "early engagement" that seeks to solve most recovery-process problems *before* they occur, and thus leaves fewer opportunities for the often unjustified intrusion of political and economic interests.

My recommendations?: (1) the Endangered Species Act must be updated to allow recovery planning to function in a way that is effective (see Table 1); (2) the recovery planning process itself must be modified to reflect our increased understanding of the ecology of threatened and endangered organisms, and the ways in which humans disturb this ecology; and most importantly, (3) fundamental changes must be effected in our society's perceptions of the relationships between business and private property on the one hand, and ecosystem (and human) health and the survival of our nation's biological heritage on the other. Sadly, I must admit that I am not unduly optimistic that any of these reforms will be seriously undertaken before we have irrevocably lost much of what Noah worked so hard to save...

TABLE 1. Some suggested reforms for improvement of the recovery planning process mandated in the Endangered Species Act of 1973, as amended in 1988. (* marks actions that would be *indirectly* beneficial.)

Suggested action	Description of reform
(1) Amend Section 4 (b)*	Under "Listing Priorities"—consideration must be given to species whose protection will reduce the need to list other species dependent on the same ecosystem.
(2) Amend Section 4 (b)*	Critical habitat designation should be released from requirement of economic impact assessment, an unnecessary delay in what is supposedly a biologically-based decision.
(3) Amend Section 4 (f)	Recovery plan development and implementation should take place within three years of listing.
(4) Amend Section 4 (f)	Recovery plans must delineate ecological, social, and economic consequences of species recovery or loss in enough detail to permit recovery options to be considered accurately by agencies and the public.
(5) Amend Section 7*	USFWS practice of differentiating alterations of critical habitat that would hurt a species chances for recovery from those that would imperil its survival are illogical—amendment should specify that "recovery" and "survival" have equivalent connotations.
(6) Amend Section 7 (b)*	USFWS must publically provide biological rationale for their concurrence with any other agencies' "no adverse effects" decisions in proposed actions potentially damaging to listed species or habitats.
(7) Amend Section 11, Change USFWS policy*	Priorities (and penalties) for treatment of vertebrates, invertebrates and plants should be equalized.

Literature Cited

- Barker, R. 1993. Saving all the parts. Reconciling economics and the Endangered Species Act. Island Press, Washington, D.C.
- Chadwick, D.H. 1995. Dead or alive. The Endangered Species Act. National Geographic 187:2-41.
- Craighead, J.J. 1994. Testimony. 8pp., in: U.S. Congress. Senate. 1994. Endangered Species Act Reauthorization—Ronan, MT. Hearing before the Committee on the Environment and Public Works. U.S. Government Printing Office.
- Dwyer, L.E., D.D. Murphy, and P.R. Ehrlich. 1995. Property rights case law and the challenge to the Endangered Species Act. Conservation Biology 9:725-741.
- General Accounting Office. 1988. Endangered species—management improvements could enhance recovery program. Washington, D.C.
- _____. 1992. Endangered Species Act: Types and number of implementing actions. Briefing report to the Chairman, Committee on Science, Space and Technology, House of Representatives. Washington, D.C.
- Hawken, P. 1993. The ecology of commerce. HarperBusiness. New York, New York.
- Keiter, R.B. 1989. Taking account of the ecosystem on the Public Domain: Law and ecology in the Greater Yellowstone region. University of Colorado Law Review 60 (4).
- Maxwell, J. 1992. Closing the salmon circle. Audubon. September-October issue.
- Meyer, S.M. 1994. The final act. The New Republic August 15, 1994: 24-29.
- Murphy, D., D. Wilcove, R. Noss, J. Harte, C. Safina, J. Lubchenco, T. Root, V. Sher, L. Kaufman, M. Bean, and S. Pimm. 1994. On reauthorization of the Endangered Species Act. Conservation Biology 8:1-3.
- O'Connell, M. 1992. Response to: "Six biological reasons why the Endangered Species Act doesn't work—and what to do about it". Conservation Biology 6:140-143.
- Northern Spotted Owl v. Lujan, 758 F. Supp. 621 (W.D. Wash. 1991).
- Rohlf, D.J. 1991. Six biological reasons why the Endangered Species Act doesn't work—and what to do about it. Conservation Biology 5:273-282.
- Schemske, D.W., B.C. Husband, M.H. Ruckelshaus, C. Goodwillie, I.M. Parker, J.G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology 75:584-606.
- Tear, T.H., J.M. Scott, P.H. Hayward, and B. Griffith. 1993. Status and prospects for success of the Endangered Species Act: A look at recovery plans. Science 262:976-977.
- _____. 1995. Recovery plans and the Endangered Species Act: Are criticisms supported by data? Conservation Biology 9:182-195.
- United States Fish and Wildlife Service. 1990a. Policy and guidelines for planning and coordinating recovery of endangered and threatened species. United States Department of the Interior, Fish and Wildlife Service. Washington, D.C.
- _____. 1993a. Recovery plan for *Serianthes nelsonii*. U.S. Fish and Wildlife Service, Portland, Oregon.
- _____. 1993b. Recovery plan for the Mauna Kea silversword (*Argyroxiphium sandwicense* ssp. *sandwicense*). U.S. Fish and Wildlife Service, Portland, Oregon.
- _____. 1993c. Mount Graham red squirrel recovery plan. U.S. Fish and Wildlife Service, Arizona Ecological Services State Office, Phoenix, Arizona.
- _____. 1994a. Recovery plan for four plants of the Lower Apalachicola Region, Florida: *Euphorbia telephioides* (Telephus spurge); *Macbridea alba* (white birds-in-a-nest); *Pinguicula ionantha* (Godfrey's butterwort); *Scutellaria floridana* (Florida skullcap). U.S. Fish and Wildlife Service, Atlanta, Georgia.
- _____. 1994b. Desert tortoise (Mojave population) recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon.
- Winckler, S. 1993. Stopgap measures. Atlantic 269:74-79.
- Yaffee, S.L. 1982. Prohibitive policy: Implementing the federal Endangered Species Act. MIT Press, Cambridge, Massachusetts.

Book Reviews

Environmental Policy and Biodiversity

R. Edward Grumbine (editor), 1994, Island Press.
(\$45.00—hardcover; \$22.00—softcover)

Conservation biologists have been warning us of a biodiversity crisis for more than a decade now. I, for one, believe them. But every time I encounter this warning, I become slightly less focused on the substantive elements of the loss of biodiversity and more skeptical of the political value of crisis scenarios. They may promote paralysis and cynicism rather than activism. The contributors to *Environmental Policy and Biodiversity* attempt to take us from the crisis scenario to solutions.

Editor Edward Grumbine contends that to address the biodiversity crisis, we must examine both our public policies and cultural practices and assumptions. The book is intended to provide policy makers access to important research in conservation biology and to offer scientists more perspective on policy making. Toward those ends, Grumbine has collected eighteen articles and conducted three interviews. Six of the chapters were written especially for the book, the remaining twelve have appeared previously in journals. The book is divided into four parts.

The first section is perhaps the strongest in the book. It includes key works on the principles of conservation biology and the application of those principles to the design of conservation reserves. Appropriately, this section is heavy on Michael Soulé, including his, "What is Conservation Biology?"; a co-authored piece with Daniel Simberloff, "What Do Genetics and Ecology Tell us About the Design of Nature Reserves?"; and an interview that addresses the key contributions of conservation biology, its implications for the practice of conservation, and the values underlying the discipline. My guess is that many readers of *Northwest Science* will have read these articles in the journals. Aside from the closing interview with Soulé and a three-page introduction, Grumbine provides no overview of the conservation biology literature, nor any treatment of the broader influence of the discipline during the last decade.

The second section examines legal aspects of biodiversity conservation. Its most substantial chapter is Robert Keiter's analysis of public land law and ecosystem management. Keiter argues that the statutory framework of the public lands systems includes numerous provisions that obligate land managers to seriously consider elements of ecosystem management. That is, managers are compelled to address biological diversity, endangered species preservation, transboundary relations and processes, and inter-agency cooperation. Other chapters in this section assess the Endangered Species Act (Daniel Rohlf, Michael O'Connell) and examine the role of conservation biology in the development of a body of law protecting ecosystems (Walter Kuhlmann). The section concludes with an interview with David Wilcove of the Environmental Defense Fund in which the ecologist discusses the adequacy of environmental laws with respect to the protection of biodiversity. Wilcove defends the Endangered Species Act as a limited but key tool and argues that science plays an important but secondary role in the development of public policy.

Grumbine collected five case studies for the third section. These examine ecosystem management issues in the Southeast, Midwest, and Pacific coast. From my perspective, the most interesting exchange in the volume appears in the two conceptual chapters opening this section. In "The Wildlands Project," Reed Noss articulates a set of principles that ought to guide "wilderness recovery and large-scale land protection" in North America (p.233). In a response, Lynn Maguire argues that key works by proponents of the Wildlands Project imply both biocentric values and the primacy of conservation biology in the development of conservation policy and practice. Maguire argues that the project is more likely to be successful if it can accommodate different values, recognize the uncertainty associated with conservation scenarios, and treat science as one among many inputs to public policy decisions.

The collection's fourth section analyzes political and administrative dimensions of conservation. It comprises two chapters addressing knowledge and uncertainty in conservation policy, one chapter assessing the prospects for a para-

digm shift in resource management, and an interview with Bonnie Phillips-Howard on conservation biology, grassroots environmentalism, and conservation policy.

Grumbine concludes the volume by raising three issues he sees as central to modern society and the imperatives of the biodiversity crisis. These issues encompass human rationality, the role of science in addressing the biodiversity crisis, and the pace of social change. While this chapter ranges more broadly than its five pages can comfortably accommodate, Grumbine seems to argue that cultural change is necessary and that a culture that connects people to place is most likely to support conservation of biological diversity.

Environmental Policy and Biological Diversity raises important issues and does so from a broad range of perspectives. Its contributors warn us of the biological diversity crisis, define principles for the design of reserves, offer critiques of conservation law, describe insights gained from real-world conservation efforts, and suggest attributes of policy-making processes that will facilitate conservation of biological diversity. The book ranges across disciplines associated with conservation biology and public policy analysis, though missing is any attempt at economic analysis.

Unfortunately, the collection achieves only one of the goals Grumbine set for it. The first section offers policy makers strong and fairly accessible scientific analyses of biological diversity conservation. But this book does not offer the best social science has to offer. Neither the "core cultural assumptions" that Grumbine finds crucial (p.xiii) nor alternative decision-making institutions are systematically addressed. Grumbine refers to cultural assumptions critically in several

places, but the collection lacks any serious analysis. Such work is available and one can only wonder why there is no environmental sociology or anthropology included. Similarly, the treatment of institutions in this book is less than adequate. Grumbine cites research on common property systems in passing, and this research has important implications, but none of the chapters analyze the relation between property arrangements and conservation. Finally, the Grumbine and Clark chapters on policy repeatedly refer to the policy sciences and postpositive policy analysis. But these discussions take place at such a high level of abstraction that it is unlikely that readers will gain much understanding of the methods or objectives of policy analysis, postpositive or otherwise. It is even less likely that readers will come away from the book with a sense of what the policy sciences have to contribute to the analysis of biodiversity policy.

If you would like to read a collection of key works on conservation biology and several short case studies, take a look at this book. If you want to see what the social sciences, or the policy sciences, have to offer with regard to conservation of biological diversity, look elsewhere. Contributors to journals, such as, *Society and Natural Resources*, *Journal of Environmental Management*, and others address elements of this problem that are only alluded to in *Environmental Policy and Biodiversity*.

— Debra J. Salazar
Department of Political Science
Western Washington University
Bellingham, WA 98225-9802
SALAZARD@henson.cc.wvu.edu

These American Lands

Dyan Zaslow and T.H. Watkins, 1994, Island Press, Washington, DC

"In the United States, there is more space where nobody is than where anybody is." This quote from Gertrude Stein begins a chapter in *These American Lands*, but it could as well begin the book itself, as it seems to fit its largely historical perspective. Unfortunately, many of the places where nobody was in Gertrude Stein's day are now places where people are. Another quote also comes to mind: "Nostalgia just isn't what it used to be" (unknown). The current United States Congress, with its values and interpretations of history that conflict with the Wilderness Society, make nostalgia understandable, but also remind us that we are not all nostalgic for the same things. In any case, it seems safe to say that the United States of 1995 and into the 21st century is and will increasingly be a very different place than has ever existed. This is important to keep in mind, because the issues and arguments recounted in this book (even the players in a general sense) are similar to those of today. The context of today's debate, however, is certainly nothing like it was in the 1800s and early to mid-1900s. The backward focus of the book significantly distracts from its usefulness today, and readers must largely find their own way to connect the history presented here with current debates, not to mention possible future courses.

Because of this, *These American Lands* falls short of its stated purpose: to combine the past and present in a coherent narrative, to discuss in detail and with authority the many problems afflicting the nation's public lands, and to present a blueprint for the future management of the public land legacy. The failure is particularly troublesome, given that this is a revised edition intended to add new content which fills the gap between the first edition of 1985 and the present.

The book is organized into chapters on National Parks, National Forests, lands managed by the Bureau of Land Management, National Wildlife Refuges, the National Wilderness Preservation System, the National Wild and Scenic Rivers and National Trails Systems, and national interest lands in Alaska (justifiably treated as a special case). There is an appendix that lists major public land

legislation and also one with a selected bibliography.

There is another appendix with yet more references for additional reading. While the authors characterize these references as merely a selection from the many additional readings available, there still seem to be significant omissions, given the subject matter of the book. The most current and thought provoking writings on the interactions between society's demand for material wealth and its view of the value and purpose of nature and wild lands are not included. Titles such as *Discordant Harmonies* by Daniel Botkin or *Beyond Preservation* edited by Dwight Baldwin et al. are not referenced. These omissions reflect a lack of attention to the intense dialogue currently occurring between the ecological sciences and our rapidly evolving cultural values.

The same shortcoming occurs in the sections of the main body which are intended to offer a course for the future. These "blueprints" sections, included in all of the chapters, are the weakest parts of the book. They are cursory at best; some are sketchy outlines without enough detail to clearly convey what it being proposed. This is particularly surprising, given the role of the Wilderness Society in recent scientific and political controversies surrounding federal lands and their management. Few would contest that the Wilderness Society remains one of the most prominent voices in the current national debate regarding the value and fate of federal lands. Unfortunately, *These American Lands* captures almost none of the recent history, current ecological thinking, or evolving cultural views of wild lands and nature. It offers only a small and not particularly persuasive piece of the substantial literature that the Wilderness Society itself has produced on these topics.

Regardless of your political persuasion, the book is invaluable as a thorough and easily useable reference for the Wilderness Society's view of the history of federal lands and of the issues that have surrounded them in the past. Besides attention to major and not-so-major laws and regulations, there are thorough discussions about the evolution of important American concepts such as federal versus state rights regarding wildlife and wildlife habitat. The key individuals that influenced the establishment and evolution of the major federal agencies are all here in vivid detail, as are the agencies themselves along with

their quarrels, infights, and triumphs. The reader can even follow the history of relatively obscure agencies, for example you can track the ups and downs (though not the current downs) of the Biological Survey and its transformations within the Department of Interior.

Despite some of the aforementioned shortcomings, the appendices are for the most part excellent. They are a real resource for quick reference to the book's primary chronology of laws and actions, and they offer many valuable references for additional reading. There's even an inventory of Wilderness, Wild and Scenic River, and Park designations made since 1985 (since the first edition of the book). The index is outstanding; it covers and cross-references not only major

topics, events, and individuals, but also many secondary or even minor ones.

Although this book falls short of its ambitious purposes, it is a key reference which should be in the library of anyone seriously interested in federal lands and the policies and management applied to them. *These American Lands* would be as useful for the members of our current Congress as to an environmental activist. It may not offer a clear proposal for the future, but it surely offers the opportunity to learn from the past.

— Susan Sater
USDA Forest Service
Pacific Northwest Region
PO Box 3623
Portland, Oregon 97208

Species Diversity in Ecological Communities

R.E. Ricklefs and D. Schluter (eds.), 1993,
University of Chicago Press

Understanding what generates and maintains diversity of species is a topic that has long challenged ecologists. With the current conservation emphasis on biodiversity we see this challenge being shifted to managers of parks and preserves without an adequate ecological model on which to base their management tactics. The occasion of this book is thus very timely. *Species Diversity in Ecological Communities* is an excellent synthesis of a number of approaches to ecological research on species diversity. While the "answer" to conserving biodiversity is not found in a simple conclusion within this book, all readers will come away with a better understanding of the multitude of factors, and the diversity of scales of factors, that strongly influence assemblage diversity. The authors are generally American and male, but nonetheless reflect a broad set of perspectives. This collection of 30 chapters is divided into an introduction and 4 general sections that reflect different scales of investigation. The sections are: 1. Local patterns and processes (5 chapters); 2. Coexistence at the mesoscale (5 chapters); 3. Regional perspectives (10 chapters); and 4. Historical and phylogenetic perspectives (9 chapters).

The editors indicate in the preface their view of the general theme of the book: "This book grew out of our conviction that the discipline of community ecology would benefit from a broadening of its paradigms. Ecological studies of the past thirty years have presumed that interactions among populations within small areas are the fundamental forces regulating community structure. However, this paradigm failed to solve one of the monumental problems of biology: the origin and maintenance of global patterns of biodiversity. Our hopes... are that the book will provide a summary statement of the discipline for researchers actively concerned with diversity issues; that it will serve as a basis for discussions and seminars for graduate students in ecology; that it will help shift the collective opinion of ecologists to a more balanced view of the factors responsible for glo-

bal patterns of biodiversity; that it will help bring about a reunion between community ecology and evolutionary biology, systematics, biogeography, and paleontology." After reading this collection, I think that the editors have more than succeeded in their goals. This should help in generating better ecological research on species diversity, and especially in generating more discussion about the diversity of factors involved.

Overall, the articles are well-written and integrated, yet the personalities of the different authors remain fresh and unique. A number of the earlier chapters take modeling approaches, whether presented in detail or hidden with only results and interpretations presented. These chapters really help to clarify many of the general issues associated with competing hypotheses about diversity at different scales and habitats of inquiry. Other chapters are more traditional in their approach of reviewing, but nonetheless remain quite appealing from the uniqueness of the author's commentaries or their insights. Especially enjoyable are the first chapter reviewing the history of research on diversity by the editors Schluter and Ricklefs, a chapter on intertidal zone diversity by Underwood and Petraitis, Rozenzweig and Abramsky's review of the relation between productivity and diversity, and Cadle and Greene's chapter on the role of phylogeny in issues of diversity. In these chapters the personalities come clearly out in a personable manner. Perhaps the summary of the book can best be encapsulated by a quote from the editors in their introduction: "These endeavors will require a broadening of the concept of the ecological community and the incorporation of novel kinds of data into community analysis."

The section on local patterns and processes includes the traditional approaches to developing models of species diversity. Tilman and Pacala review 7 theories of the maintenance of local species richness. They use a modeling approach as well, and show us only the results rather than the underlying mathematics. They focus on the general categories of processes allowing persistence of numerous species (e.g., spatial and temporal heterogeneity) and processes that limit diversity (e.g., small population size, limiting similarity, habitat flux). They conclude that actual constraints and trade-offs have not been identified in most habitats and that we need to link models of persistence with models of extinction.

Underwood and Petraitis provide an incredibly interesting and stimulating paper that critiques assumptions of small scale studies. They begin by reminding us that often ecological studies assume that sufficient small-scale experimentation will lead to more general or large-scale understanding of the outcome of ecological processes. Yet "nowhere has there been an attempt to evaluate the degree to which the quantitative outcomes of experiments of various designs and power, on populations with different histories and different spatial and temporal variations of abundances, are comparable or even commensurable. To date, no one has provided evidence that accumulation and synthesis of numerous small-scale studies is a valid method for interpreting general or larger-scale patterns" (p. 39). This paper does a great job illustrating the difficulties of comparing processes among studies, and of the importance of processes of different scale, and of local unique historical events. These difficulties include not only ecological processes (e.g., predation, exposure to waves) but also methodological (size of experiments, duration, timing). It provides general guidelines toward making future studies more readily comparable. Overall, it is a really excellent chapter, because it not only synthesized ideas together but also provided a critique of our current progress.

The section on coexistence at the mesoscale focuses on larger scale processes, on spatially structured landscapes of habitat patches, and explore the implications of population interactions in subdivided landscapes for diversity within landscapes. Holt begins this section with a strong chapter on the role of regional processes. Holt models how we can conceptually understand mesoscale processes, those processes between local (traditionally studied) and large scale (geographic and long temporal). Using a source pool/sink models Holt provides a clear and interesting approach to spatial and temporal aspects of heterogeneity at these scales. I was particularly interested in the article by Hanski, Kouki and Kalkka because of the diversity of publications on range/abundance relationships in the last 10 years. They start off with a clear organization of the many scales at which researchers have approached this question, a "clearing of the air" which has been needed. But while they pose 3 possible explanations, they focus on one of them that they have modeled, metapopulation dynamics. On the other hand, they give a clear and interesting perspective on this rela-

tionship (range/abundance) and its role in diversity.

The third section is the largest and it really provides a more detailed look at particular examples from a variety of perspectives, from insect diversity on bracken fern worldwide, specialized biological groups like tiger beetles, freshwater fish parasites, or pelagic diversity, to larger scales like the Mediterranean region and the continent of Australia. The objective of the section is to examine patterns of diversity within biogeographical regions or within particular taxa, "emphasizing the empirical basis of diversity phenomena, assessing the principle of community convergence, and evaluating various explanations of diversity patterns." This section seems the most eclectic to me, but that's just the nature of the topic. As an example, the article by Lawton, Lewinsohn and Compton on patterns of diversity for insect herbivores on bracken fern seems like a narrow topic. Yet the authors have worked on bracken herbivores for a number of years in a variety of places. The result is an insight into general influences on species diversity through the lens of bracken herbivores. They provide a table of factors at the end of their analysis that summarizes their findings, which are primarily that history (continents, past vegetation change) and plant host range (within the region or continent) were the strongest "effects" on patterns of insect diversity.

The final section sets out historical and phylogenetic approaches to studying the development of ecological communities, using information from systematics, biogeography, and paleontology to reconstruct the history of diversity within regions. I found this section particularly interesting, principally because it is refreshing to see these perspectives in a collection of ecological articles. Cadle and Greene wrote a great article that emphasized the importance of phylogenetic information for community studies. They focused on neotropical snake assemblages. Because they have researched the phylogenetic relationships among the different clades of snakes found in the neotropics, they compare their interpretation of patterns of diversity in different locations with how a standard "ecological process" interpretation would view the diversity. The result is an obviously more powerful view of snake assemblages as compared with classical ecological interpretations separated from

phylogenetic information. Lathan and Ricklefs similarly present an interesting approach to their analysis of continental comparisons of temperate-zone tree species diversity. This article investigates north-temperate forest tree diversity comparing North America with Europe and Asia. By using a simple process called "rarefaction", in which more diverse floras were randomly reduced in size to match species numbers in less diverse floras, they were able to compare diversity at the level of genera, families, orders and subclasses; along with a comparison of fossil floras from the same regions. The result is an interpretation that differences in diversity expressed among the regions really results from patterns at higher levels of taxonomy rather than simply the species level. They concluded that the primary difference between Asia and the more depauperate North American and European floristic diversity (diversity at higher taxonomic levels) is old and probably was established by regional differences in

colonization and autochthonous production of new taxa. This suggests that the origin of the diversity was much older than the more recent periods of contraction and extinction experienced in North America and Europe. The diversity concentrated in Asia results most likely from a continuum of temperate-tropical habitats, resulting in a corridor lacking in the other locations.

In conclusion, this lengthy book (414 pages, large pages with small type), even though it fails to touch on the nth degree of detail, is quite comprehensive and very successful, especially in emphasizing one important point. That point is that diversity at any location must be considered from a balanced perspective resulting from processes acting at different scales.

—V. Thomas Parker
Department of Biology
San Francisco State University
1600 Holloway Ave.
San Francisco, CA 94132

Ecophysiology of Coniferous Forests

William K. Smith and Thomas M. Hinckley (eds.), 1995, Academic Press, \$74.95

The aim of physiological ecology is to explain plant distribution on the basis of the interrelationship between plant structure and function and the physical environment. The approach has been largely individualistic in nature. In *Ecophysiology of Coniferous Forests*, Smith and Hinckley have assembled a group of papers in an attempt to integrate traditional individualistic approaches of ecophysiology with coniferous forest distribution, past, present and future.

The chapters, by a diverse number of international authorities, cover a range of topics encompassing genetic variation, past distribution, various aspects of basic ecophysiology, effects of herbivores and pollutants to potential effects of global climate change on coniferous tree and forest distribution. Each chapter could easily be a lengthy book itself. Thus each chapter is a review of the current state of knowledge and directions of particular areas of research. In total the book provides the reader with a very good sense of where ecophysiology fits into understanding and predicting patterns of distribution of conifers.

Chapter one reviews the relationship of genetics to physiological ecology of conifers from common garden studies through allozymes to molecular techniques. Conifers possess a high degree of genetic variability both among and within populations, but with some exceptions and contradictions. The chapter concentrates on Rocky Mountain studies, but gives an excellent flavor of the range of genetic work that has and is being done.

Chapter two relates past climate and variation in the distribution of conifers both geographically and altitudinally in north American and Europe. The emphasis is on effects of past climate on distribution of species at various time scales from decades to millennia. The authors conclude that species tend to react individually to climate change, and this can lead to very different and surprising assemblages. Chapter three examines the effect of hormones on physiological processes. The bulk of studies discussed deal

with abscisic acid (ABA) because of its relation to stomatal control, gas exchange and water relations. Problems with quantification are dealt with briefly. The chapter then deals with models which relate water transport and ABA concentration and finishes with a discussion of the influence of climate on ABA and stomatal operation. Because little work has been done on conifers, much of the data are from herbaceous plants. Looking at chemical control in woody plants and conifers is sorely needed.

Chapter four addresses some morphological and physiological characteristics of conifers which enhance their abilities in high latitude climates. Emphases in the chapter are on xylem structure and ability of needles to recover from cold temperatures. A problem with trees in cold climates is cavitation and embolisms in the xylem due to freezing. This is a problem in spring, where xylem must be repaired for growth of leaves to occur. Conifers, lacking large vessels appear less likely to develop embolisms, and thus have a potential for growth earlier than woody angiosperms. Needle recovery must also be fast. The importance of mycorrhizae in high litter, low nutrient soils is discussed.

Chapter five covers winter characteristics of conifers which allow them to endure long winters and respond rapidly during the short growing season. The importance of winter hardening and enduring winter desiccation are discussed. Signals which cause the onset of hardening, and their importance are reviewed along with evidence for endogenous rhythms. Hardening is discussed at the membrane and cellular levels. Alterations to water relations, photosynthesis and respiration in winter are summarized.

Chapter six, one of the two longest of the book deals with insect herbivory and conifers. This chapter, compared with the others, has a lot of detailed information. The authors deal with a thorough review of determinants of nutrient levels in plant tissues before dealing with the herbivore interaction. The chapter seemed somewhat chopped up compared to the others. It might well have been better to have two chapters, one dealing with nutrient acquisition, both carbon and mineral (although a companion volume, *Resource Physiology of Conifers* arising from the same workshop, is out), and a chapter dealing with insects relationship to conifers. Insect herbivory is

shown to have both negative and positive effects depending on conditions. Some mention of vertebrate effects would have been nice.

Chapter seven deals with foliage dynamics. Models, such as the pipe model, which relate sapwood and leaf area are discussed to set the stage for physical limitations. Then modifications of leaf area due to crown geometry, growth rate and genetics are discussed. Finally, stand leaf area effects and remote sensing of stand leaf area are dealt with.

Chapter eight covers leaf life span variation. The authors emphasize early on that conifers possess a range of leaf life spans from months to decades, and thus can not be uniquely separated on this basis, sharing a broad overlap with angiosperms. The approach to leaf life span dynamics is through its association with nutrient acquisition, carbon balance and environment. The separation of genetic vs. environmental components is also an important component. The inverse relationship between nutrient availability and leaf longevity has been reported for a long time, but more recent work on photosynthetic nitrogen-use efficiency and nitrogen turn over have helped to further understand leaf life span dynamics. Because trees with 5 year leaf life spans require different conditions than trees with 10-15 year leaf life spans, the authors argue that it is important that leaf life span not be treated as deciduous vs. evergreen, but rather leaf life span be treated as a continuous variable.

Chapter nine, which along with six, is the longest chapter in the book, deals with effects of pollution on conifers. The chapter narrowly focuses on the effects of ozone, justifying that its effects act directly at the leaf level, rather than at both leaf and root level, and that sulfur and nitrous oxides have been dealt with extensively elsewhere. The authors deal with uptake processes and progress to cellular and leaf level effects of ozone. They progress to leaf senescence, whole plant effects and the effects of ozone at the stand level. Finally they report on models which attempt to predict results of ozone on various levels of organization within conifers and conifer communities. By dealing with a single pollutant they are able to present in depth both approaches to and results of work on the interrelationship between conifers and pollution.

Appropriately, the final chapter (10) looks at the potential effects global climate change may have on the distribution of conifers. This of course reflects the ultimate goal of science, which is to understand nature well enough to make accurate predictions about what happens if we perturb the system. Of course making predictions is only as good as the understanding and the data available. In ecology, when dealing at the community level, both are at their infancy. On top of this, climate predictions on a global scale are still very general. I think we can safely assume that carbon dioxide will increase, but what else occurs, especially at regional levels is highly speculative within a wide range of probabilities. In this chapter, the authors using various climate predications talk about tree level to geographic level outcomes based on known interactions and global models. The modeling approach discussed works at distribution levels of coniferous forests based on alterations of WUE (water-use efficiency) resulting from elevated CO₂, changes in temperature and wind speed. In addition they discuss possible implications in nutrient pool and carbon balance as a result of changes in conifer dominance. The bottom line of the chapter, and perhaps the book, is that we have a long way to go, even though in some areas we have a very good start, to connecting small scale (cell, leaf) ecophysiology to large scale (plant, community, ecosystem) understanding.

For someone who wants an up to date (references as late as 1994) treatise on aspects of conifer ecophysiology, the book is excellent. All chapters have extensive bibliographies. The chapters are directed and thus, the reader will not get a broad overview of topics, but will get good insight into direction and approaches at a variety of scales. Most of the chapters read easily and develop ideas linearly. Only the chapter on herbivory seemed to take a long time to get to the point, but did present some very valuable information. The book is intended for researchers in conifers and not for forest managers. The book is recommended reading for anybody interested in plant ecophysiology. The price, while high, is reasonable for Academic Press.

—David H. Hansen
Dept. of Biology
Pacific Lutheran University
Tacoma, WA 98447-0003

Conservation and Management of Neotropical Migrant Landbirds

David S. Dobkin, 1994, Univ. of Idaho Press, Moscow, Idaho (\$29.95)

During the past several years there has been a growing body of evidence that suggests that many species of song birds have been declining in their breeding range, particularly in the eastern United States. Data for the western United States are not as complete. The purpose of this publication is to "serve as an integral part of efforts aimed at understanding the present population status and conservation needs of the Neotropical migrant landbirds that breed in the northern Rockies and Great Plains."

This publication provides an overview of the status and current knowledge of species breeding in the geographic region that coincides with Region 1 of the U.S. Forest Service which includes eastern Washington, northern Idaho, Montana, North Dakota, South Dakota and northern Wyoming. Over 75 percent of the slightly less than 200 species that breed in this region are Neotropical migrants, that is, birds that breed in Canada and the United States but winter in Mexico, Central or South America or the islands in the Caribbean. Typical Neotropical migrants include most species of warblers, flycatchers, hummingbirds, vireos, thrushes, swallows and some species of sparrows and other finches. This publication consists of five major parts that include the Introduction, Survey of Management Activities and Impacts in the Northern Region, Habitat Profiles, Explanation of Species Accounts, and Species Accounts.

The Introduction provides the reader with some valuable background information on historical declines in forest birds of the eastern United States and very quickly points to forest fragmentation as the primary culprit contributing to the decline of Neotropical "forest interior" nesters. The two primary detrimental effects associated with forest fragmentation are the effect of predation by species of vertebrates associated with forest edges, and the effect of brood parasitism by the brown-headed cowbird. The Breeding Bird Survey (BBS) provides the primary data available for documenting long-term breeding bird population trends in

western North America. The second major contributor to population declines is the apparent adverse effects of deforestation in the Neotropics. The final part of the Introduction discusses the status of birds in western North America. The BBS and other data are inadequate for many areas, but what is available seems to indicate that the avifauna is not suffering from widespread declines found for many species in the East. This is primarily because of the fundamentally different nature of the western United States which is topographically more diverse than the eastern United States. Forest fragmentation in the West is the result primarily of timber harvesting with the potential for regeneration rather than from forest loss and conversion which tends to be typical of eastern forests. The author correctly points out that our knowledge of population changes in the West is relatively poor and more research is needed to examine the nature of habitat changes and how birds respond to them.

The section on management activities is a brief literature review of the effects of management on birds in coniferous forests, deciduous forests, riparian zones and grassland-shrubsteppe. Riparian zones are also discussed. In the discussion of forests, some topics covered were bird response to forest fragmentation, cowbird brood parasitism, silviculture, fire effects, and livestock grazing. Similar topics were addressed in the other habitat types.

The Habitat Profiles section was a brief depiction of the major habitats discussed by using illustrations of habitat profiles. On these profiles, bird species were shown as they occupy vertical locations in the habitat based on either nesting or feeding locations. This should help readers with little ornithological background understand the importance of forest structure and possibly tree or shrub species composition to bird foraging and nesting opportunities.

The Explanation of Species Accounts includes the parts of a table that lists the family or subfamily, species name, and wintering area of the Neotropical migrants in the region. It provides an overview of all species covered.

The Species Accounts section comprises the bulk of this publication. With each account there is a statement of the residency status, wintering area, habitat requirements, feeding, status and management, further reading, and a rather crude

range map of the species distribution within the region. Each account is one page in length. Finally, there is a table showing the occurrence of each of 144 bird species in the 12 habitat types described for this region.

The author states that this publication "establishes a proactive approach to the management of species by assessing the state of our current knowledge and activities before populations dwindle to the point of no return." The former and current status is presented but a final analysis that would summarize how many species are declining, increasing or showing no change in population status would have been helpful. Most species appear to increase in some parts of the region while either decreasing or show no change in other parts of the range. However, some criteria could have been used to make judgments so that an overall picture of the region could be made and then perhaps compared with other regions of the United States.

The Literature Cited section contains over 600 references which should be helpful to readers wishing to get more details on various aspects of this subject.

The range maps are very crude and of limited value. Maps with habitat types or topographic features would have added some value. The authors apparently used but did not cite the A.O.U. Checklist of North American Birds (Sixth Edition and supplements) for scientific names.

Overall, this publication will help managers and wildlife biologists in Region 1 to be more aware of the status of Neotropical birds and what factors may cause declines in their abundance and distribution.

—David A. Manuwal
Wildlife Science Group
College of Forest Resources
University of Washington
Seattle, WA 98195

Honorary Life Members

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